

Cyclocarya brownii from the Paleocene of North Dakota, USA

by

Malcolm DeWitt Taylor

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Graduate Supervisory Committee:

Kathleen B. Pigg, Chair
Martin F. Wojciechowski
Melanie L. DeVore
Jack Farmer
Anthony Gill

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ABSTRACT

The Juglandaceae (walnuts, hickories, pecans) has one of the best-documented fossil records in the Northern Hemisphere. The oldest modern genus, *Cyclocarya*, today restricted to China, first appears in the late Paleocene (57 ma) of North Dakota, USA. Unlike walnuts and pecans that produce edible fruits dispersed by mammals, *Cyclocarya* fruits are small nutlets surrounded by a prominent circular wing, and are thought to be wind- or water-dispersed. The current study provides the first evidence that fossil fruits were different from modern forms in the number and organization of their attachment to reproductive branches, and in their anatomical structure. Unlike the modern genus that bears separate pistillate and staminate flowers the fossil fruits had attached pollen-bearing structures. Unisexual pollen catkins are also present, suggesting the fossil *Cyclocarya* may have differed from its modern relative in this feature. Like several other plants from the late Paleocene Almont/Beicegel Creek floras, *Cyclocarya* shows a mosaic combination of characters not seen in their modern counterparts.

Fossils were collected from the field, and examined for specimens exposed on the weathered rock surface. Specimens from Almont were photographed with reflected light, while those from Beicegel Creek cut into slabs and prepared by etching the rock matrix in 49% hydrofluoric and re-embedding the exposed plant material in cellulose acetate and acetone to

make "peels". Selected specimens are cut out, mounted on microscope slides, and studied with light microscopy.

These fossil fruits were studied because they are the earliest fossil evidence of *Cyclocarya*. They are exceptionally preserved and thus provide critical structural evidence for changes in that occurred during the evolution of plants within this lineage. Because *Cyclocarya* fruits are winged, they might be assumed to be wind-dispersed. Their radial symmetry does not have the aerodynamic qualities typical of wind-dispersed fruits, and may have been dispersed by water.

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Chapter 1

INTRODUCTION

This study documents new information about the fossil record of *Cyclocarya* Iljinskaya, a living monotypic genus in the walnut family (Juglandaceae). These fossils, with greater morphological and anatomical preservation than those known previously, are being studied to gain a greater insight into character evolution within the clade in the Juglandaceae that includes *Cyclocarya* and its living and fossil relatives. The present study will attempt to gain a broader overview of the historical biogeography of the genus from the seemingly North American nexus to its present day distribution in southeastern China. The fruits of *Cyclocarya* first appear in the late Paleocene of North America, followed by occurrence in the early Eocene of Europe, as *Juglandicarya depressa* Reid and Chandler of the London Clay (Manchester, personal communication 2010). Fruits of *Cyclocarya* are represented in multiple Eocene and Oligocene sites of Eurasia. They next appear in the Miocene of Japan and finally in the extant range of China today. Finally, since we now have a greater number of fossil fruits from the best-preserved Paleocene species, *Cyclocarya brownii*, a brief discussion of dispersal mechanisms and the biomechanics of the fruit can be addressed. This can also be directly compared to the extant species and new insight shed on potential modes of wind and water dispersal of these distinctive winged fruits.

The Juglandaceae is an economically important group of trees and shrubs native to temperate hardwood forests, and higher elevations in the Subtropics valued for wood and edible fruits, including walnuts (*Juglans* L.) and pecans (*Carya* Nuttall, Heywood, 1993). Oils from the nuts are used in cosmetics, soaps and as a drying agent in paints. This family is ecologically important in providing fruit for local foragers, and also contains one of the most well documented cases of allelopathy in the black walnut *Juglans nigra* L. (Bode, 1958). The phytochemical produced by *Juglans*, Juglone, is found in the leaves, roots, bark, and husks of the genus. It is highly toxic or growth stunting to neighboring plants.

The family is distributed primarily in temperate and subtropical zones of China and North America (Fig. 1). In the Eastern Hemisphere, the family extends into India and Malaysia, while in the Western Hemisphere the family has evolved primarily in North America and into higher elevations of Central America and northern South America (Graham, 1999). Today the family is recognized as having nine genera and 60+ species (Manos and Stone, 2001) and is divided into two subfamilies (Table 1). Subfamily Juglandoideae contains the genera *Platycarya* Siebold and Zuccarini, *Juglans*, *Pterocarya* Kunth, *Cyclocarya* Iljinskaya and *Carya*. Of these, *Carya* and *Juglans* are cosmopolitan in the Northern Hemisphere, and *Pterocarya*, *Platycarya*, and *Cyclocarya* are exclusively Asian today (Lu, 1982). The second subfamily, Engelhardioideae, includes the Asian genus *Engelhardia* (commonly misspelled as *Engelhardtia*, a

mistake corrected by Blume) Leschenault ex Blume; *Alfaropsis* Iljinskaya, which occurs in southeastern Asia; *Oreamunoa* Ørsted (formerly *Oreomunnea* Ørsted, yet another commonly misspelled genus, which Ørsted later corrected, see Wilbur, 1981), which is native to southern Mexico and Central America in montane regions; and *Alfaroa* Standley which is distributed from southern Mexico into northern Columbia. These genera are well defined and supported by both molecular and morphological data (Stevens, 2001, onwards; Manos et al., 2007; Manchester et al., 2009).

Members of the Juglandaceae are large, deciduous, semi-evergreen or evergreen trees (rarely shrubs) with alternate (occasionally opposite), pinnately compound leaves, either petiolate or sessile (Heywood, 1993). Leaves are aromatic, nonsheathing and estipulate, and may contain domatia. Plants are usually monocious (rarely dioecious), with typically unisexual flowers borne in catkins or sometimes solitary; inflorescences may be racemes, spikes or panicles. Staminate flowers bear triporate to stephanoporate pollen with fine, evenly distribution spinulose ornamentation (Stone and Broome, 1975). Pistillate flowers are two-bracteolate, bracteolate or ebracteolate, with bractlets often adnate to bracts, forming the husk-like involucre that surrounds the fruit. Fruits are nuts, or small nutlets, and while the best-known edible fruits, such as walnuts, are large nuts that lack wings, several important genera have smaller nutlets with prominent wings (*Engelhardia*, *Pterocarya*, *Cyclocarya*). Wings can be either

three (*Engelhardia*), two (*Pterocarya*) or, in the case of *Cyclocarya*, a single circular wing envelops the nutlet.

Higher order classification—The family Juglandaceae has held a changing phylogenetic position within higher taxonomic groups over time (Manos and Stone, 2001; APG II, 2003; APG III, 2009; Table. 1). Originally, Juglandaceae (Fagales) were part of a group of woody dicots with small, unisexual catkins bearing wind-dispersed pollen known as the Amentiferae (Stern, 1973). Other members of the Amentiferae included the Myriciales, Uricales, and Salicales (Wolfe, 1973). These groups were long known to be placed together, based on artificial similarities, but no revision was attempted until the late 1960's.

Takhtajan (1967) established a classification scheme for the dicots in which he proposed six subclasses within Class Magnoliopsida. Subclass Hamamelididae included most of the plants previously referred to Amentiferae (Stern, 1973). Within this framework Cronquist (1968, 1988) proposed the Order Juglandales within Hamamelididae and named the two families Juglandaceae and Rhoipteleaceae to the order. Cronquist (1968, 1988) also included in the Subclass Hamamelididae the orders Trochodendrales, Hamamelidales, Daphniphyllales, Didymelales, Eucommiales, Urticales, Leineriales, Myricales, Fagales, and Casaurinales. The Hamamelididae was informally divided into the “higher” and “lower” grades, with Juglandales included in the higher Hamamelididae based on flower and pollen morphology (Kubitzki et al., 1993). Cronquist (1968, 1988)

and several others (e.g., Wolfe, 1973; Friis, 1983) noted the similarities between the pollen in higher Hamamelidae with that of the Normapolles pollen found in the Cenomanian of the Cretaceous. Cronquist (1968, 1988) also noted that the pinnately compound leaves were a feature unique to the Juglandales within the group. Wolfe (1973) documented the unusual foliar morphology of Juglandales and suggested that the order be removed from the subclass Hamamelidae. He suggested that the foliar morphology of Juglandales shows a relationship with the rosids. This concept was further supported by Hufford (1992) who demonstrated that Juglandaceae is a crown group within the core rosids, and sister to Myricaceae and Casuarinaceae.

The modern systematic concept was developed in the late 1980's with cladistic studies of the so-called "lower" Hamamelididae (Crane and Blackmore, 1989). Cladistic analyses of Trochodendrales (Hufford and Crane, 1989), Fagaceae (Nixon, 1989) and the group as a whole (Hufford, 1992) concluded that the "lower" Hamamelididae was neither monophyletic, nor at the base of a subclass. The "higher" Hamamelididae consisting of Juglandales, Myricales, Casuarinales, and the families of Betulaceae, and Nothofagaceae were found to nest within the rosids (Hufford, 1992).

Molecular analyses supported Juglandaceae as a sister group to Rhoipteleaceae and concluded that these two families in turn form a sister group to Betulaceae, Ticodendraceae, Casuarinaceae and Myricaceae (Manos and Stone, 2001). Currently, the Angiosperm Phylogeny Group (APG II, 2003; APG III,

2009) recognizes the same nine families as Manos and Stone (2001) within Fagales, but advises that *Engelhardia* may be paraphyletic and more observation is needed to resolve this question.

History of systematics of Juglandaceae— The systematics within the family has changed throughout the literature since the mid-twentieth century (Manos and Stone, 2001; Stevens, 2001 onwards; Manos et al., 2007, Table 1). Originally, Leroy (1955) proposed two subfamilies for Juglandaceae, the Oreomunnoideae containing *Platycarya*, *Pterocarya*, *Engelhardia*, *Oreomunna*, and *Alfaroa*, and Juglandoideae with *Juglans*, *Carya*, and *Annamocarya* Chevalier (= *Carya*). Manning (1978), using mainly flower and fruit morphological characteristics, proposed Platycaryoideae containing only *Platycarya*, with all of the other genera placed in Juglandoideae. He divided Juglandoideae further into three tribes: Juglandae [*Juglans*, *Pterocarya* (which included *Cyclocarya*)], Engelhardieae (*Engelhardia*, *Oreomunna* and *Alfaroa*) and Hicorieae (*Carya*, including *Annamocarya*). Schaarschmidt (1985) named two subfamilies, the Platycaroideae with the two tribes Platycaryeae (*Platycarya*, *Carya*) and Engelhardieae (*Engelhardia*, *Oreomunna*, *Alfaroa*), and the Juglandoideae (*Juglans*, *Pterocarya*, and *Cyclocarya*). Manchester (1987), studying the Tertiary fossil record, recognized Manning's Juglandae and Hicoreae, and moved *Carya* into Hicoreae, and placed *Juglans*, *Pterocarya* and *Cyclocarya* in the Juglandae. Iljinskaya (1993) reorganized Manchester's classification into three subfamilies:

Platycarioideae (without the recognition of the tribe Platycaryeae), Engelhardioideae (including the new genus *Alfaropsis*), and Juglandoideae, with the tribes Juglandae and Hicorieae.

Phylogenetic analyses within Juglandaceae based on combined morphological and molecular data that were conducted by Smith and Doyle (1995) included phylogenetic analysis of chloroplast DNA restriction site variation using *Betula* L., *Quercus* L., and *Myrica* L. as the outgroups. The results of this study showed that *Juglans* was sister to *Pterocarya* with those two genera forming a sister clade to *Carya* and *Platycarya* being the outgroup to this grouping. This group makes up the subfamily Juglandoideae. *Oreomunna* and *Alfaroa* were sister taxa to *Engelhardia* which formed a second subfamily Engelhardioidae within the Juglandaceae. These two clades support the classification of three subfamilies within the Juglandaceae, as previously outlined by Manchester (1987) and later by Iljinskaya (1993). Although both Manchester (1987) and Iljinskaya (1993) included *Platycarya* in a separate subfamily, it is not a large leap of faith to see this in the cladogram produced by Smith and Doyle (1995). *Platycarya* occurs between the two currently recognized subfamilies of Juglandoideae and Engelhardioideae and could easily be recognized as a separate subfamily.

Manos and Stone (2001) later corroborated these results with findings based on morphological and chemical characters, cpDNA, and ITS sequences. They produced a cladogram showing *Cyclocarya*, *Pterocarya*, and *Juglans*

forming a group, however this is not very well resolved and a trichotomy is formed. This group in turn, forms a clade sister to *Carya* (which would presumably include *Annamocarya*). These genera form the tribe Juglandae, with *Platycarya* (tribe Platycaryeae) as the sister group. Together these five genera (or six including *Annamocarya*) form the subfamily Juglandoideae. The second subfamily in the Juglandaceae, Engelhardioideae, consists of a clade that contains a crown group of *Alfaroa*, *Oreamunoa* and *Alfaropsis* Engelhardia. Using molecular techniques, Manos and Stone (2001) named two subfamilies, the Engelhardioideae with *Engelhardia*, *Oreamunoa*, *Alfaroa*, and *Alfaropsis* and the Juglandoideae with three tribes: Platycaryeae (*Platycarya*), Juglandae with two new subtribes Juglandinae (*Juglans*, *Pterocarya*, *Cyclocarya*), and Caryinae [*Carya*, (*Annamocarya*)].

The changing classification systems of genera within Juglandaceae are the result of several factors. First, there was the recognition of *Alfaropsis*, a new Asian genus with features intermediate between the New World genera *Alfaroa* and *Oreamunoa* and the Old World genus *Engelhardia* (Iljinskaya, 1993; Stone, 2010). Additionally, several segregate genera were proposed within the family (*Annamocarya*, *Cyclocarya*), that were originally recognized by some authors (e.g., Iljinskaya, 1953) and not others (e.g., Manning, 1975, 1978). Since the early 2000's the addition of characters from molecular studies, and new information from the fossil record have further contributed to the framework upon which to base classification and to our current understanding of the family's

phylogeny (Manos and Stone, 2001; APG II, 2003; Friis et al., 2006; APG III, 2009; Stone, 2010).

Fossil record of Juglandaceae— For this study, the family Juglandaceae is defined in the sense of Manos et al., 2007, including both fossil and extant genera recognized therein. The family has a rich fossil record including fruit, pollen catkins, leaves, pollen, and wood (Manchester, 1987; 1999, Wheeler and Manchester, 2002; Chen et al., 2009). All members of both subfamilies are represented in the record, especially in regards to fruit and seed fossils. In particular, the fruit record, dating back to the Paleocene, documents the early evolutionary history and the diversity of the family (Manchester, 1984, 1999; Stevens, 2001 onwards; Manos et al., 2007).

Fruits—Late Cretaceous mesofossils from several sites in eastern coastal North America and Europe have been assigned to the order Juglandales (Friis et al., 2006). Genera such as *Manniniga* Friis, *Antiquocarya* Friis and *Caryanthus* Friis are bisexual and found in close association with or containing Normapolles pollen, a feature often associated with Juglandaceae because of the similarities of Normapolles grains with those of extant forms within the family. Features place these genera in the order Juglandales but the fossils cannot be assigned any closer since they have features common to both Juglandaceae and Rhoiptelaceae. One

Cretaceous mesofossil, *Budvaecarpus* Crepet, Nixon and Gandolfo, has been assigned formally to the Juglandaceae (Crepet et al., 2004).

In the Paleocene, Juglandaceae is known from western North America and Far East Russia (Manchester and Dilcher, 1982; 1997; Manchester et al., 1994; Manchester 1999; Kodrul and Krassilov, 2005). The oldest of these occurrences is *Amurcarya* Kodrul and Krassilov from the early Paleocene of Far East Russia. This genus is based on fruits with an orbicular wing similar to *Cyclocarya*; however, the wing is lobed and has a different venation pattern. Other features of *Amurcarya* suggest it is assignable to Engelhardioidae rather than Junglandoideae like *Cyclocarya* (Kodrul and Krassilov, 2005)

In western North America the extinct genus *Polyptera* Manchester and Dilcher, is recognized from two localities in the Fort Union Group of Wyoming (Manchester and Dilcher, 1982). *Polyptera* is characterized by a multilobed, disk-like wing and pyramidal nutlet. *Cyclocarya*, also known from the Fort Union group but in younger strata, has occurrences in North Dakota, Wyoming and Colorado. *Cyclocarya brownii* Manchester and Dilcher, the subject of this current study, occurs in the late Paleocene Almont and Beicegel Creek, North Dakota sites. Manchester (1987) illustrated and briefly mentioned fruits from near Broadus, Montana, suggesting they might also represent *C. brownii*. One poorly preserved fruit referred by Hickey (1977) to *Pterocarya hispida* Brown ex Watt (Plate 15, fig. 9 of Hickey, 1977) is known from the Bear Den Member of the Golden Valley Formation. This specimen has a partially preserved wing and a

central nutlet, however it is unclear without additional examination whether it can be identified conclusively. It is figured along with a “juglandaceous leaf fragment” (Plate 15, fig. 10 of Hickey, 1977). In comparison to *Cyclocarya brownii*, two other species are known from western North America. *Cyclocarya minuta* Manchester and Dilcher was described from the late Paleocene of Wyoming, and *Cyclocarya coalmontensis* Manchester and Dilcher from the latest Paleocene of Colorado. These fossil fruits are assigned to *Cyclocarya* based on nutlet morphology, but the wing is either incompletely preserved or missing. Additional species of *Cyclocarya* are known from throughout Eurasia in the Oligocene (*Cyclocarya cycloptera*, *Cyclocarya tymensis*, *Cyclocarya tavidensis*, and *Cyclocarya tompskiana*), and the Miocene (*Cyclocarya ezoana* Manchester, 1987) (Figs. 3-4).

Another genus, *Juglandicarya* Reid and Chandler is known from both the western North American Fort Union Group and British Paleogene, where it was originally described from the London Clay (Reid and Chandler, 1933; Manchester, 1987). *Juglandicarya simplicarpa* (Manchester, 1987), preserved as locule casts in siltstone and also from the Fort Union group is thought to have close affinities with extant *Carya* on the basis of a smooth, thick shell and locule casts with both primary and secondary septa. *Juglandicarya depressa* Reid and Chandler and *J. lubbocki* Reid and Chandler are known from the early Eocene London Clay of southern England (Reid and Chandler, 1933). *Juglandicarya depressa* is quite similar and possibly even congeneric with *Cyclocarya* (S. R.

Manchester, personal communication, 2010), while *Juglandicarya lubbocki* is reported to have affinities to extant *Carya* (Reid and Chandler, 1933).

The Eocene saw a radiation of the family and the first appearances of fruits assignable to several other extant genera. The first occurrence of modern *Carya* is found during the late Eocene in Eastern Europe. In the Florissant Formation of Colorado, *C. florissantensis* Manchester is associated with juglandaceous foliage. The only other appearance of *Carya* in North America occurs in the middle Miocene of Washington, *C. washingtonensis* Manchester (Manchester, 1987). This species was named for a large mass of over 50 silicified fruits that were found together in association with a hollow *Platanus* log, and interpreted as a fossilized nut cache (Manchester, 1987, Fig. 34). Also in North America, the first occurrence of *Pterocarya*, *P. macginitii* Manchester and Dilcher, occurs in middle Eocene strata of Wyoming. *Pterocarya* persists in North America until the Miocene when it goes extinct there, but makes its first appearance in Eurasia. It is currently found as an Asian endemic (Lu, 1982; Chen et al., 2009). In addition to evolution within Juglandoideae, the early and middle Eocene of North America saw a large radiation in the Engelhardioidae. There are twelve species of *Palaeocarya* Saporta. This genus shares a conglomerate of characters with both *Engelhardia* and *Oreamunna* and persists from the late Eocene to Miocene in both North America and Europe. Two other related genera that appear in the middle Eocene of eastern North America are *Paraengelhardtia* Berry and *Paleooreomunna* Dilcher, Potter and Crepet. These genera are also

associated with the Engelhardioidae, but are only known from the middle Eocene Claiborne Formation of Tennessee (Dilcher et al., 1976; Manchester, 1987).

The first appearances of *Platycarya* and closely related genera are in the Eocene. *Platycarya richardsoni* Reid and Chandler and *Pterocaryopsis* spp. Chandler are known from the London Clay deposit of southern England and from North America, in addition to *Hooleya* Reid and Chandler (Reid and Chandler, 1926, 1933). *Pterocaryopsis richardsoni* is the name for the infructescence and *Pterocaryopsis* is the name given to the dispersed seeds, which have not been assigned to a species as of this point. *Hooleya*, occurring later in the London Clay, is a large winged platycarioid seed. Genera assignable to the *Platycarya* lineage are also known from the early Eocene of North America. *Platycarya americana* Hickey and *Paleoplatycarya wingii* Manchester from Wyoming and North Dakota, respectively, show the characteristic lateral bi-winged fruits that which are diagnostic for the group (Manchester, 1987). An extinct juglandaceous fruit, *Beardia* Elliott, Mindell, and Stockey is also known from the Eocene of Vancouver Island, British Columbia, Canada (Elliott et al., 2005). This genus has been interpreted as having transitional characters between the two subfamilies.

Later Tertiary occurrences of both subfamilies of the Juglandaceae fruits and seeds demonstrate changes in biogeographic distribution (Manchester, 1987, 1999). *Cyclocarya* first appears in the Paleocene and extends into the Eocene of North America. In Europe it is known from possibly early Eocene (as *Juglandicarya* in the London Clay, Manchester et al., 2009), then also occurs

there from Oligocene to Pliocene. The genus first appears in Asia during the Oligocene, where it remains present today. The earliest occurrence of the closely related *Pterocarya* is in the Oligocene to Miocene of North America, it ranges from the Oligocene to Recent in Europe, and from the Miocene onwards in Asia. *Juglans* is first known in the North American Eocene, and then becomes cosmopolitan in the Northern Hemisphere from the Oligocene on. It is not found in Eocene deposits of North America, but this may be a product of sampling. *Carya* appears in the Eocene of North America, and then remains in North America and Asia today. *Platycarya* first appears in the Eocene of North America and Europe, and then is unknown until its appearance in Asia where it is extant today.

Leaves — The record of fossil juglandaceous leaves is reviewed by Manchester (1987). Fossil leaves attributed to Juglandaceae in late Paleocene sites of western North America were described by Brown (1962) and referred to *Pterocarya hispida* Brown. Although this name refers to fruits of the genus *Pterocarya*, leaflets with this general morphology have been found occasionally at the Almont site (Crane et al., 1990). Most recently, fossil leaves assigned to *Cyclocarya* cf. *paliurus* have been described from the middle Eocene of China (Sun, et al., 2005).

Woods— Fossil woods of the Juglandaceae have been described from many sites (Manchester, 1983; Wheeler and Manchester 2002; Blokhina, 2007; Wheeler and Dillhoff, 2009). In western North America two wood genera are described from the middle Eocene Clarno Nut Beds as *Clarnoxylon blanchardii* Manchester and Wheeler and *Engelhardtioxylon nutbedensis* Manchester and Wheeler. *Clarnoxylon* is an extinct genus based on the presence of a solid pith and crystal-bearing idioblasts in the rays and lacking scalariform perforations. This genus is thought to be related to the *Palaeoplatycarya* fruits. *Engelhardtioxylon* differs from *Clarnoxylon* by the presence of occasional scalariform perforation plates and lack of crystal-bearing idioblasts. The middle Miocene fossil woods at Vantage, Washington include two species of the wood type *Rhysocaryoxylon* Dupéron, *Rhysocaryoxylon tertarium* Prakash and Barghoorn and *Rhysocaryoxylon fryxellii*. Both of these species resemble the wood of North American black walnuts but lack the reticulate vessel elements typically characteristic of extant *Juglans* (Wheeler and Dillhoff, 2009). However, modern *Juglans* wood analyzed by Miller (1976) was found to lack this feature in woods found at low latitudes. Based on this finding among extant forms, Wheeler and Dillhoff (2009) suggested that a similar situation might be present in the Vantage woods.

Pollen — Many authors have noted the similarity of extant pollen of Juglandaceae with a distinctive type of spore assemblage called the

Normapolles Complex (Pflug, 1953; Wolfe, 1973; Friis, 1983; Friis et al., 2006). This group of dispersed pollen types is found throughout eastern North America and Europe from the middle Cenomanian but mostly vanishing by the middle Eocene. There are over 80 species of fossil pollen named in this complex and it is commonly recognized as an index fossil for the Normapolles Province. This area is well constricted to the eastern part of North America and Europe until the Maastrichtian, where the grains begin to appear in western North America and Asia (Srivastava, 1981). Normapolles pollen grains are triporate, and characterized by elaborate thickened walls around the pores, and a distinctive, regular pattern on the exine of small spinules.

Pollen similar to that of extant Juglandaceae is common and diverse in many Tertiary palynomorph floras of western North America where it has played an important role in biostratigraphy. In the Williston Basin, the zonation of Nichols and Ott (1978) is based in large part on changes in the assemblages of juglandaceous grains (Zetter et al., in press). Pollen of the *Momipites* type (also known as *Maceopollenites*) is known in situ from catkins associated with *Polyptera* (Manchester and Dilcher, 1997). Several types of juglandaceous pollen are known from the Almont matrix (Zetter et al., in press), and one distinctive type has been found in anthers attached to some fruits of *Cyclocarya*, as discussed below.

Extant *Cyclocarya* —Within the Juglandaceae, the genus *Cyclocarya* which is endemic to the mountains of China contains a single species, *C. paliurus* (Batalin) Iljinskaya (Flora of China, accessed, 1 October 2008). These ~30 m tall trees have odd-pinnate leaflets with serrate margins. The inflorescences are monecious, pendulous and both lateral and terminal, with separate male and female flowers (Figs. 17a-c; 18b). The fruits of *C. paliurus* are borne pendulously with a 2-4 chambered nutlet surrounded by a wing (Fig. 17a, c). The nutlets are round and compressed with a diameter of 7 mm on average. The surrounding wing is leathery, orbicular to ovate, highly vascularized, and range from 2.5 – 6 cm in width (Iljinskaya, 1953).

Originally, this species was treated in the genus *Pterocarya*, but after further investigation by Iljinskaya (1953) the new genus of *Cyclocarya* was proposed and the species placed within. The species *Pterocarya paliurus* was then renamed to *Cyclocarya paliurus* by Iljinskaya. This reassignment was based on the lack of *Pterocarya* generic characteristics that *C. paliurus* had and the difference in the way the wing is formed. Originally, *C. paliurus* was thought to have formed its circular wing by fusing the two separate wings found in *Pterocarya*. Iljinskaya (1953) observed the development of flower to fruit in *C. paliurus* and noted that this was not the case, but that this wing is presumably formed from the bracteoles. The proposal of this new genus was argued in the literature, and *Cyclocarya* was not a widely accepted genus until the mid 1980s.

The current study—In 1982, Manchester and Dilcher first formally described fossil *Cyclocarya brownii* from the original Almont site. In this study they documented details of fruit morphology, including the nutlet and wings, from a combination of fractured surfaces and ground serial sections. In 1987, Manchester noted that some fruits had been discovered with long pedicels (Manchester, 1987 Fig. 39b). Crane et al. (1990) illustrated additional specimens, including one showing a pedicellate fruit (Crane et al. 1990, Fig. 18 C), and another that was fractured in oblique longitudinal view, showing the attachment of the nutlet (Crane et al., 1990; Fig. 18 G).

During the interval of time from 1990 until around 2007 additional specimens of *Cyclocarya* were collected from the original Almont site, and from around 2000-2007 more became available from the newly discovered Beicegel Creek locality. These new fossils increased the number of specimens from an original seventeen specimens upon which the Manchester and Dilcher (1982) study was based to several hundred. The present study includes 101 fruits. In addition to a larger number of specimens found, the new specimens provide considerable new morphological and anatomical information that form the basis for the present study.

At the same time, from around 2000-2007, new phylogenetic studies appeared, based on combined morphological and molecular data (Doyle and Smith, 1995; Manos and Stone, 2001) and incorporating the known fossil record (Manos et al., 2007). Additionally, new information has emerged about

distribution, ecology and seed germination of extant *Cyclocarya* (Flora of China, accessed 1 October, 2010; Fang et al., 2006). Together these studies provide a framework with which to understand newly discovered information about fossil *Cyclocarya*.

The present study will document new information about *Cyclocarya brownii* fruits in the following ways: (1) Infructescences with attached fruits are described for the first time, and compared with those of extant *Cyclocarya paliurus* and discussed in relation to character evolution within the genus (2) An understanding of the wing attachment to the fruit is resolved on the basis of anatomically preserved specimens; (3) Anatomical details of the fruit wall are characterized for the first time from Beicegel Creek specimens prepared with cellulose acetate peels; (4) The taxon is emended to include these new features; and (5) Fruit dispersal of *Cyclocarya* is investigated in relation to what is known about the biomechanics of winged diaspores. The addition of this new information greatly increases our understanding of both the fossil and extant forms of *Cyclocarya* and its significance to the evolution and phylogeny of Juglandaceae as a whole.

Figure 1. The current distribution of the subfamilies within the Juglandaceae showing the dominant Northern Hemisphere distribution (after Stevens, 2001 onward).

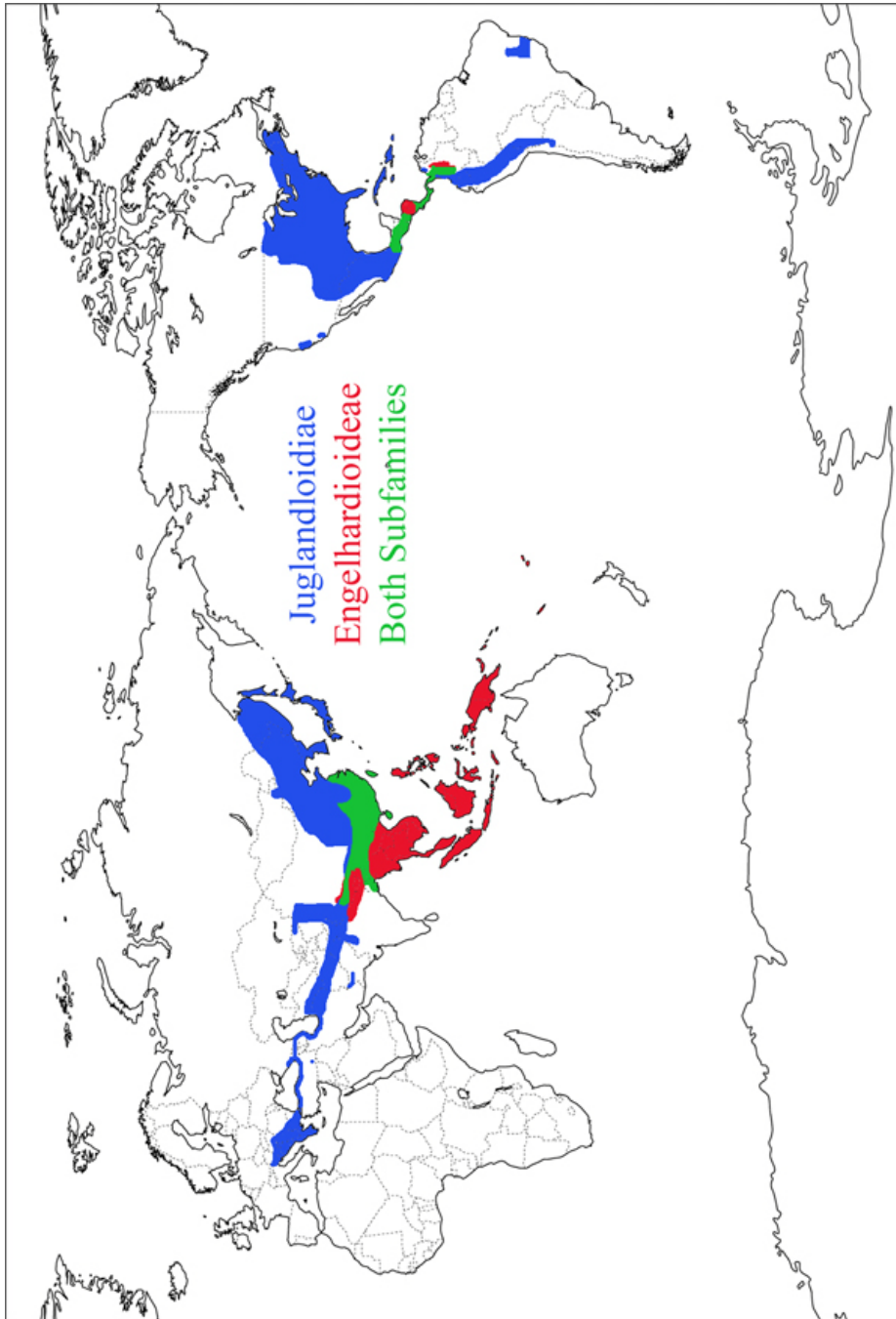


Figure 2. A simplified cladogram showing the currently accepted relationships of the genera within the Juglandaceae, as well as the relationship of the Juglandaceae to the other families within the Fagales (after Manos et al., 2007).

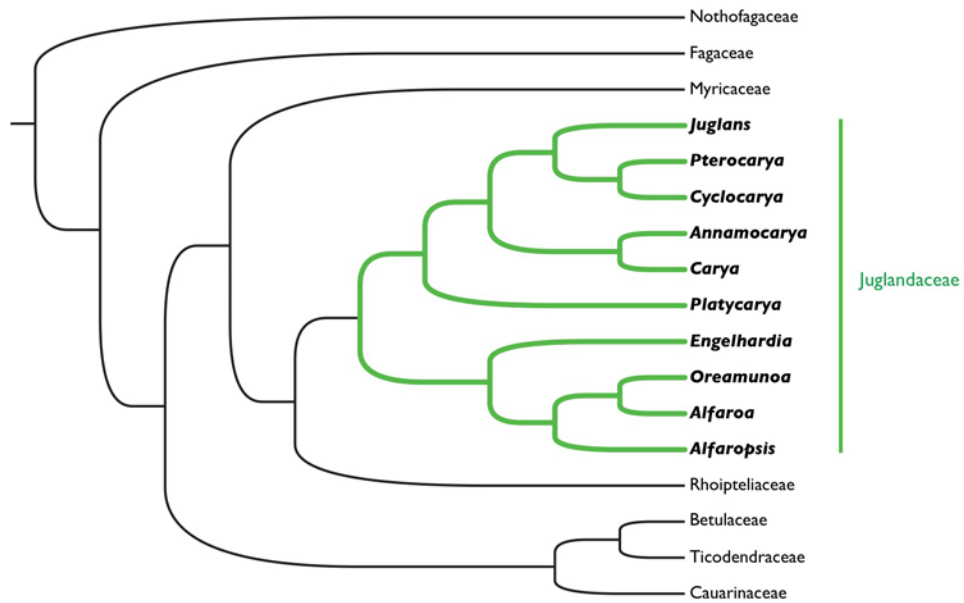


Figure 3. The global fossil distribution of *Cyclocarya*, with *Juglandicarya* included, as it may be congeneric (Redrawn from Manchester 1987).

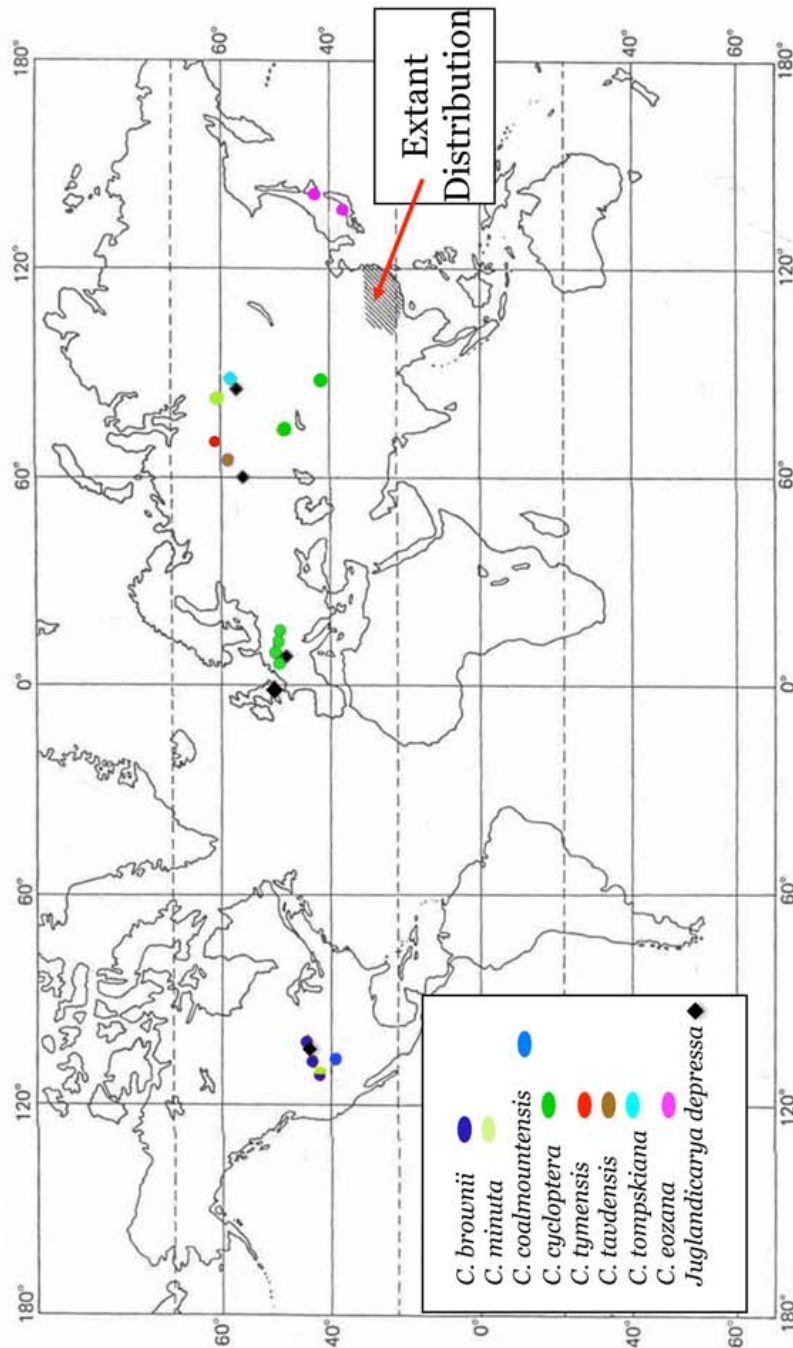


Figure 4. The occurrences of fossil members of *Cyclocarya* during the Cenozoic plotted across the Northern Hemisphere. The oldest known fossils of the genus are in North America, then appear in Eurasia, and are solely in Asia by the Miocene. The current distribution is in montane regions of China.

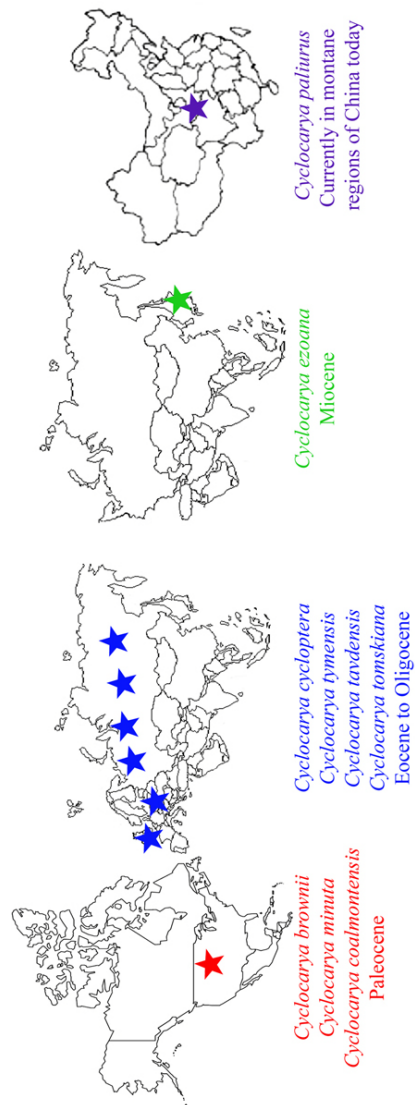


Table 1. The historical and current views of the relationships between the genera of the Juglandaceae (after Manos et al., 2007).

Leroy (1955)	Manning (1978)	Schaarschmidt (1985)	Manchester (1987)	Ilijinskaya (1991, 1993)	Manos and Stone (2001)
OREOMUNNOIDEAE Platycarya Pterocarya Engelhardtia Oreomunnea Alfaroa	PLATYCARYOIDEAE Platycarya	PLATYCARYOIDEAE PLATYCARYEAE Platycarya Carya	PLATYCARYOIDEAE PLATYCARYEAE Platycarya	ENGELHARDIEAE Engelhardtia Oreomunnea Alfaropsis Alfaropsis	ENGELHARDIOIDEAE Engelhardtia Oreomunnea Alfaroa Alfaropsis
JUGLANDOIDEAE Juglans Carya Ammanocarya	JUGLANDOIDEAE JUGLANDEAN Juglans Pterocarya	ENGELHARDIEAE Engelhardtia Oreomunnea Alfaroa	ENGELHARDIEAE Engelhardtia Oreomunnea Alfaroa	JUGLANDOIDEAE JUGLANDEAE Juglans Pterocarya Cyclocarya	JUGLANDOIDEAE PLATYCARYEAE Platycarya
	ENGELHARDIEAE Engelhardtia Oreomunnea Alfaroa	JUGLANDOIDEAE Juglans Pterocarya Cyclocarya	JUGLANDOIDEAE JUGLANDEAE Juglans Pterocarya Cyclocarya	HICOREAE Carya	JUGLANDEAE JUGLANDINAE Juglans Pterocarya Cyclocarya
	HICORIEAE Carya Ammanocarya		HICOREAE Carya	PLATYCARYOIDEAE PLATYCARYEAE Platycarya	CARYINAE Carya Ammanocarya

Chapter 2

MATERIALS AND METHODS

Localities— The *Cyclocarya brownii* fossils studied come from two late Paleocene sites in North Dakota. They are both located within the Williston Basin (Fig. 5), the easternmost and largest of a series of basins in western North America (Pigg and DeVore, 2010). This basin extends from North Dakota in the east to Montana in the west. The northern extent of this basin is found in the southern regions of the Canadian provinces of Manitoba and Saskatchewan, and the southern margin extends into South Dakota.

Depositional Setting --The Williston Basin is the largest of the western North American basins, and has a long history of deposition (Gibson, 1995). The basin originated in the Cambrian, and it had extensive deposition during the Cambrian, Silurian, and Ordovician. Deposition continued into the Pennsylvanian and Mississippian, but had mostly ended by the end of the Paleozoic. The primary sediment deposited during the Paleozoic was marine limestone and dolomite, as well as sandstones, shales, siltstones, and, to a lesser extent, evaporites. During the Mesozoic, sediments were deposited in the basin, but at a much lower volume than the Paleozoic environments. The final surge of deposition was during the end of the Mesozoic when the Laramide Orogeny “recharged” the basement features, increasing the depositional rate in the basin during the late Cretaceous through the Eocene. This last surge is of particular interest as it contains many of the plant fossil localities that extend through the

Paleocene to span the Paleocene-Eocene boundary. The sites in the present study are of late Paleocene age.

Plant fossil localities --A rich fossil record of plants is known for the Williston Basin from late Cretaceous to early Eocene strata. Among the plants the transition from the late Cretaceous floras of Hell Creek Formation (Johnson, 2002; Peppe et al., 2007) into the early Paleocene Fort Union Formation has been documented in southwestern North Dakota. Early to middle Paleocene floral change has been described for the Ludlow and Tongue River Members of the Fort Union group (Peppe, in press). The Sentinel Butte Formation contains the Almont and Beicegel floras of the present study (Manchester et al., 2004; Pigg and DeVore, 2010), as well as sites at Wannagan Creek (Melchior and Hall, 1983). The Golden Valley flora from western North Dakota (Hickey, 1977), which includes two units, the Bear Den Formation which spans the Paleocene-Eocene boundary (Clarkforkian) and the Camels Butte Formation within the early Eocene (Watachsian). In the northern part of the Williston Basin, the Ravenscrag Formation of Saskatchewan extends from Puercan to Torrejonian age (McIver and Basinger, 1993; Pigg and DeVore, 2010).

Additional late Paleocene floral sites in western North America include Joffre Bridge, Munce's Hill, and Genesee (Alberta Basin; Hoffman, 2002), and numerous localities in the Bighorn Basin of Wyoming (Wing et al., 1995) and the

Green River Basin of Wyoming, Colorado, and Utah (Wilf, 2000; Pigg and DeVore, 2010).

Collecting sites, stratigraphy, and depositional environments— Fruits examined in this study occur at both the original Almont locality in central North Dakota (Crane et al. 1990) and at the Beicegel Creek locality in the western part of the state (Figs. 5; 6a-c; 7a-d) (Pigg and DeVore, 2010). Fossils are preserved in silicified non-marine shale, located in the Sentinel Butte Formation of the Fort Union Group (Figs. 6a-c; 7a-d). The deposit is stratigraphically correlated on the basis of associated freshwater mollusks and mammals as Tiffanian-3 (Kihm and Hartman, 1991). Stratigraphically this study and previous published and informal analyses of both Almont and Beicegel Creek sites (McClain and Manchester, 2001) correlate with pollen zone P5 of Nichols and Ott (1978). The P5 zone extends from the older Bullion Creek Formation into the Sentinel Butte Formation.

The original Almont site is about 88.5 km west of the eastern edge of the Williston Basin, in Morton County approximately 3 km north of New Salem, and roughly 48.3 km west of Bismarck, North Dakota (Fig. 5; 6a-c). Fossils are excavated from shallow pits dug just below the soil in an agricultural field (Figs. 6a-c). The Almont site was originally described as a small lacustrine environment such as a small pond or oxbow lake (Crane et al., 1990), but subsequent observations have led researchers to believe it is a smaller part of a larger fluvial

system (Pigg and DeVore, 2010), perhaps representing an oxbow lake. It can be inferred that it was a low energy system based on the preservation of relatively intact leaves found at the original site (Figs. 8a-b). This low energy environment is necessary to preserve the leaves in such a way that they are not damaged mechanically due to transport prefossilization, especially in the case of *Cyclocarya*, since it has a fragile wing that would not normally be preserved (Fig. 8c).

One-hundred-and-twenty km to the northwest of the original Almont locality in Morton County is the Beicegel Creek site in McKenzie County, western North Dakota (Manchester et al., 2004). Fossiliferous shale layers at Beicegel Creek can be correlated with those of the original Almont site on the basis of lithology and plant fossil remains.

In contrast to the Almont site, the Beicegel Creek locality occurs in badlands topography. Exposures on the sides of buttes throughout the landscape provide considerably more information about stratigraphic sequences than is available from the original Almont locality (Figs. 7a-d). Several of these sites have provided fossils for the present study, including those informally referred to as “Silica Top” (Figs. 7a-b), “Kate’s Butte” (Fig. 7c), and “Two Snake Butte” (Fig. 7d). The siliceous shales are found in situ at Silica Top (Fig. 7a), and scattered throughout several additional sites. Preliminary sedimentological study by Melanie DeVore and Deborah Freile in 2007 demonstrated that the Beicegel Creek localities include fossiliferous layers within both the silicified shales and

several other lithologies. In contrast to the Almont site the overall depositional setting can be interpreted as a higher energy fluvial system (Pigg and DeVore, 2010). The energy in this system is evident in the preservation of the fossils in these localities. The fossils are mechanically damaged prefossilization, as evident by the condition we see them today (Figs. 8c-d). The material is disarticulated, and highly fractured. This would indicate that the material was transported in a high-energy system before it was deposited.

The author first visited the Beicegel Creek locality in June 2003, and again in 2004, and 2005, during which collections were made and driven back to Arizona. The author also participated in collecting at the original Almont locality during these trips.

Techniques for study—The fossils at both sites are highly silicified, and preserved in such a way to show both external morphological features and internal anatomical structure (Crane et al., 1990). The Almont specimens were identified on fractures surfaces of blocks of siliceous shale. Specimens previously studied by Manchester and Dilcher (1982) were partly from these fractured surfaces, and others were ground serially for anatomical detail, particularly of seed anatomical structure (Manchester and Dilcher, 1982). Sections studied by Manchester and Dilcher (1982) were photographed under light microscopy, with reflected light. The author visited collections including Manchester and Dilcher's (1982) type material at the Florida Museum of Natural History in 2006 and 2009, and at the

Field Museum, Chicago in 2007. The author visited the John D. Curtis Collection of Almont specimens at the University of Wisconsin at Stevens Point, Stevens Point, Wisconsin in April 2007.

Specimens in the present study were photographed directly from weathered or fractured surfaces with reflected light (Nikon D-70 camera base using a 50 mm flat-field macro lens; Nikon D-90 with phototube extension in turn on a Nikon SMZ Stereomicroscope; Nikon Inc., Melville, New York). Specimens for the present study were prepared for SEM by sputtercoating with 20 nm of platinum and mounted on SEM stubs with double-stick tape. Specimens were viewed on a Hitachi S-415A Scanning Electron Microscope (Hitachi, Tokyo, Japan) at 15kV.

Fossils from Beicegel Creek were prepared using the cellulose acetate peel technique (Joy, et al. 1956), modified for silicifications (Basinger and Rothwell, 1977), to reveal three-dimensional internal cellular detail of the plants. Specimens were sectioned with a diamond-embedded blade, and reference peels made. Additional serial peels were made of critical specimens, and mounted on microscope slides. The peels of the fossils were then used to make a direct comparison, to the fruit wall of the extant species of *Cyclocarya*.

Comparative study of fruits, leaves, and pollen catkins containing pollen was accomplished with material obtained from Der Botanischer Garten der Technischen Universität Dresden, Germany. Fruits and pollen catkins were studied with light microscopy and photographed digitally with reflected light.

Extant fruits, anthers and pollen were prepared for SEM by sputtercoating with 20 nm of platinum and mounted on SEM stubs with double-stick tape. Specimens were viewed on a Hitachi S-415A Scanning Electron Microscope (Hitachi, Tokyo, Japan) at 15kV.

History of collecting and repositories of collections— Fossils from the original Almont site, particularly *Ginkgo* leaves are known locally are prized by collectors, because of their beautiful preservation of white or dark leaves on a tan-orange matrix (Fig. 8b). The first formal paleobotanical study of the site was that of *Cyclocarya* fruits (Manchester and Dilcher, 1982). Peter Crane and his colleagues at the Field Museum and Indiana University (and later the University of Florida), including Steven Manchester and David Dilcher, first made large collections of the Almont site in the early 1990s. Substantial collections are deposited at the Field Museum and the Florida Museum of Natural History, University of Florida, Gainesville, mostly from collections made by Manchester and colleagues. Additional collections were made by botanist John D. Curtis, Professor Emeritus of University of Wisconsin at Stevens Point (UWSP), who took many student field trips to the Almont site during the 1990's and early 2000's, and his collections are housed at UWSP. Additional collections, many from private collectors, are held in the North Dakota Heritage Museum in Bismarck, ND, (John Hoganson, personal communication). Kathleen Pigg, Melanie DeVore and colleagues have made collections that are housed at ASU

since 1999. Others are in the hands of private collectors, and some specimens can be found in rock shops throughout the country.

Fossil specimens examined in the present study are housed at the Field Museum, Chicago (PP); University of Florida, Gainesville (IU- and UF, University of Wisconsin at Stevens Point (UWSP), North Dakota Heritage Museum (NDHM), and Arizona State University (ASU).

Almont and Beicegel Creek floras— Late Paleocene floras of North America, Asia and Europe were thought to be typically low diversity (e.g., Crane, 1981; Gemmill and Johnson, 1997). This low diversity was thought to be a result, partly of the vast climatic and geological changes that occurred from the Late Cretaceous, through the Paleocene (Graham, 1999). The Cretaceous saw the drying and disappearance of the seaway, which connected the Arctic Ocean with the Gulf of Mexico. The Cretaceous-Tertiary (K/T) boundary is delimited by major extinction events. Several lines of evidence suggest that many of the ecosystems in North America were disrupted by end of Cretaceous events, including a bolide impact (Nichols and Johnson, 2008). During this time an increase in volcanic activity also contributed to atmospheric changes and altered climates globally.

In contrast to the more typical late Paleocene sites, the Almont and Beicegel Creek floras are considerably more diverse (Pigg and DeVore, 2010; Zetter et al., in press). Crane et al. (1990) provided a survey of the plants found at

the original Almont site. This paper documented the unusually well preserved flora site and estimated that 30-40 species were present. Leaves, stems, and reproductive structures represented the fossils present and at the time were noted by Crane and colleagues as being angiosperm-dominated, but had only two gymnosperms and no pteridophytes. The authors noted that although there were common species that were present in most Paleocene middle to high latitude floras, there were a substantial number of novel species at this locality (Table 1 in Crane et al., 1990).

In the two decades since the initial paper was published, 20 taxa have been named formally based on megafossils, with at least an additional dozen remaining to be described, as discussed below (Manchester and O’Leary, 2010; Zetter et al., in press; Kathleen B. Pigg, personal communication, 2010).

In addition to the plant megafossils at Almont, the pollen record has also been investigated. In a recent study, pollen recovered from the original Almont matrix were prepared by the “same grain” technique, in which individual pollen grains are recovered, photographed with light microscopy and then placed on stubs and studied with Scanning Electron Microscopy (SEM) (Zetter et al. in press). These pollen grains were identified by the spore dispersal names used for stratigraphic purposes (e.g., Nichols and Ott, 1978). Where possible they were correlated with grains found in situ in reproductive structures (Zetter et al., in press). This survey resulted in the description of 50 identified taxa of pollen and spore types, representing 28 families.

Of the megafossil floral elements known from the Almont and Beicegel Creek flora, three main subcomponents can be described: 1) a typical late Paleocene low-diversity component, 2) a group of rarely occurring elements of taxonomic groups that today occur in tropical and subtropical regions; 3) an early occurrence of several genera that become more widespread in later temperate floras.

The first group of “typically low diversity” floral components known from middle to high latitude Northern Hemisphere Paleocene localities include members of Ginkgoaceae, Betulaceae, Hamamelidaceae, Platanaceae, and Cornales, as well as taxodiaceous conifers. These families have been well documented from numerous sites throughout the Paleocene of North America, Greenland, England, and China (Manchester, 1999). First of these typical Paleocene plants to be described were *Nordenskiodia* Heer and *Zizyphoides* Newberry (Trochodendraceae; Crane et al., 1991). These genera are interpreted as extinct members of the family Trochodendraceae that is today an Asian endemic group, but which has a fossil record from the Cretaceous through Miocene in western North America (Manchester, 1999).

Later that year, Manchester et al. (1991) recognized the new cornalean genera *Amersinia* Manchester, Crane, and Golovneva for distinctive fruits and *Beringiaphyllum* Manchester, Crane, and Golovneva for associated leaves at Almont and numerous other Paleocene localities in western North America, Greenland, and China. Both of these fossil species are part of the Cornales and

are found dispersed in both New and Old World sites in the Northern Hemisphere. Another member of the Cornales, the extant genus *Davidia* Ballion (Manchester, 2002a), was described from leaves, and fruits from Almont and eight additional sites of the Fort Union Group.

The Betulaceae, subfamily Coryloideae are represented in the Almont flora by a distinctive species of *Palaeocarpinus* Crane, *P. dakotensis* Manchester, Pigg, and Crane reconstructed as a whole plant from Almont and the Beicegel Creek locality based on infructescences, fruits, pollen catkins with in situ pollen and associated leaves.

Another family representative of the “low diversity” elements is the Hamamelidaceae. From this family Benedict et al. (2008) described *Hamawilsonia* Benedict, Pigg and DeVore, as an extinct genus based on infructescences, isolated fruits, some containing seeds, and pollen catkins with pollen grains of the *Retitrespolpites catenatus* Pocknall and Nichols type. Both *Palaeocarpinus* and *Hamawilsonia* are mosaic taxa that have combinations of characters not present in extant genera of their respective families.

The second floristic group includes rare occurrences of taxa in families that are currently of tropical and subtropical distribution, including Icacinaceae, Menispermaceae, Myrtaceae, and Zingiberales. Many of these early appearances of these families become significant components of floral localities that occur during the Eocene thermal maximum (Manchester, 1994, 1999).

Icacinaceae, a pantropical family now, is represented by one genus, *Icacinicarya* Reid and Chandler and two species, based on distinctive anatomy of the fruit endocarps (Pigg et al., 2008a). There is one species represented at Almont and the other at Beicegel Creek. The Icacinaceae are a group that becomes important components of the lower Eocene London Clay flora (Reid and Chandler, 1933; Collinson, 1983), and the middle Eocene Clarno Nut Beds (Manchester, 1994).

A member in the genus in the Myrtaceae, *Paleomyrtinea* Pigg, Stockey and Maxwell (Pigg et al., 1993), has been documented at both Almont and Beicegel Creek localities and represented by numerous fruits and seeds (K. B. Pigg, personal communication, 2006). This genus first appears in the Paleocene localities of North Dakota, and is a commonly found element of the early-middle Eocene Princeton Chert of British Columbia

Paleosecuridaca curtisii Pigg, DeVore and Wojciechowski (Pigg et al., 2008b) is the oldest representative of the Polygalaceae. Although this family is not strictly tropical, the genus *Securidaca* L. that it closely resembles is. Like several other Almont plants, this taxon has a combination of characters found separately in different modern taxa, (i.e. a samara-like fruit of *Securidaca* but a seed coat with typical structure of the genus *Polygala* L.).

Additional groups that today occur in tropical to subtropical sites that are currently under study include Ochnaceae (Pigg et al., 2005) and Zingiberales (DeVore and Pigg, 2005; Benedict et al., 2006, 2007).

The third group of plants includes genera that have early fruit and seed evidence in the Almont flora that become more important components of later temperate floras. These include *Cyclocarya*, *Aesculus* L., *Paleoactaea*, Pigg and DeVore, and *Cornus piggae* Manchester, Xiang, and Xiang (Manchester et al., 2010). Additional plants in this group that are currently under study include *Acer* (Kittle et al., 2006) and a member of the kiwifruit family Actinidaceae (Pigg and DeVore, 2003).

The first paper published from the original Almont locality was the naming and description of *Cyclocarya brownii* (Manchester and Dilcher, 1982). This species is the focus of the present study. It was already formally described by Manchester and Dilcher (1982) and this project is expanding their work greatly by adding more specimens, with better preservation, and a lot of additional characters of the fruits. A complete compound leaf and associated fruits of *Aesculus* (Manchester, 2002) has been documented and it was noted that it was more similar to the North American and Eastern European species than the Asian ones. *Paleoactaea*, an extinct member of the Ranunculaceae was described from the Almont locality (Pigg and DeVore, 2005) and provided a Paleocene occurrence for the family. A representative of the oldest known subgenus of the genus *Cornus*, *Cornus piggae* (Manchester et al., 2010), was recently described from the Almont locality based on well preserved silicified endocarps.

Finally, a few very rare aquatic angiosperms and ferns have been described or briefly mentioned from both the Almont and Beicegel Creek

localities. Seeds of *Nuphar* Sm. were noted from Almont (Chen et al., 2004), indicating that the two subfamilies of the Nymphaeaceae had diverged before the late Paleocene. Another genus in the family, *Susiea newsalemae* Taylor, Pigg and DeVore (Taylor et al., 2006), was described from seeds found in the Almont locality and shown the *Euryale*-lineage seeds to have diversified before the Eocene. The unusual aquatic *Porosia* (Lesquereux) Hickey is also known from both sites (Manchester, 2002b). Among pteridophytes found at Beicegel Creek but not Almont are the fern *Woodwardia* Sm. (Pigg et al. 2006; Matthews et al., 2006), and the lycopod *Isoetes* (Matthewes, et al., 2007).

Figure 5. A map of North America that shows the extension of the Williston Basin. The original site of Almont is marked by □ and Beicegel Creek is indicated with ■.



Figure 6. The original Almont site in an agricultural field showing pits dug for excavation of fossils (A-B). The “cornfield” locality 2.5km north of the original site showing the fossiliferous shale after the soil has been turned for planting, bringing the material to the surface (C).



Figure 7. The Beicegel Creek locality in McKenzie County, North Dakota. The fossiliferous layer was found in situ on the Silica Top microsite (labeled with arrow) (A-B). There are other microsites in the area containing the fossiliferous shale including Kate's Butte (C) and Two Snake Butte (D). Two Snake Butte shows a large fluvial channel preserved at the base overlain by shale.

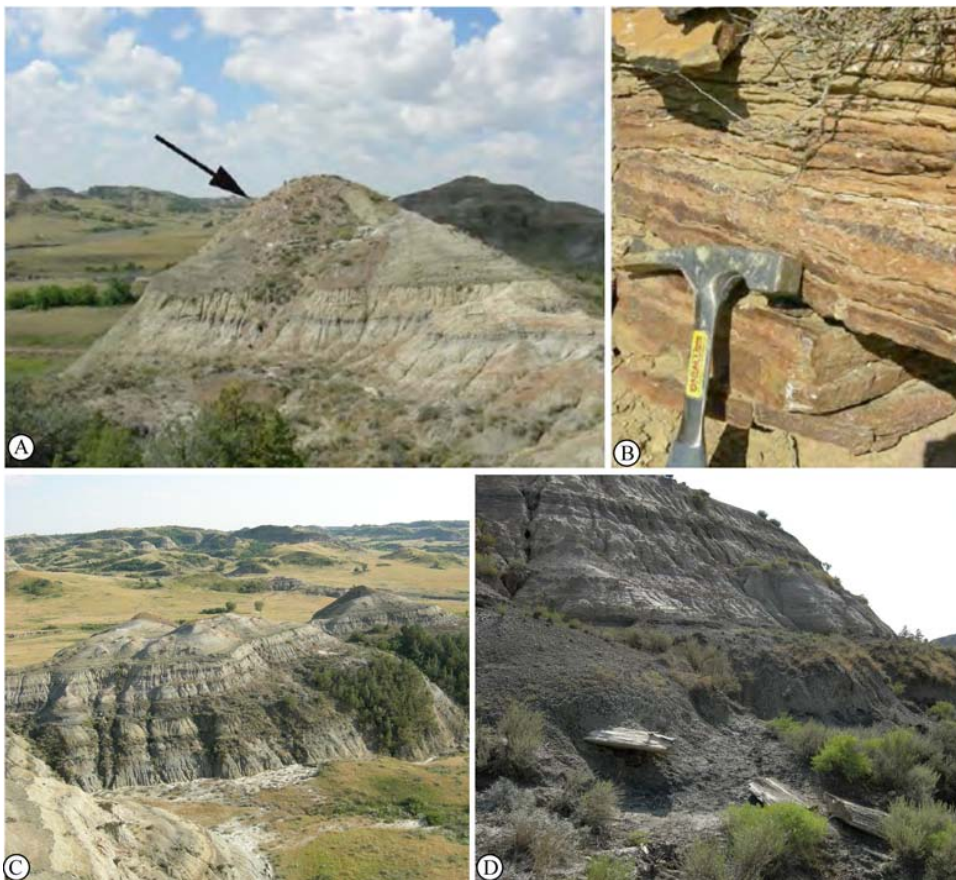
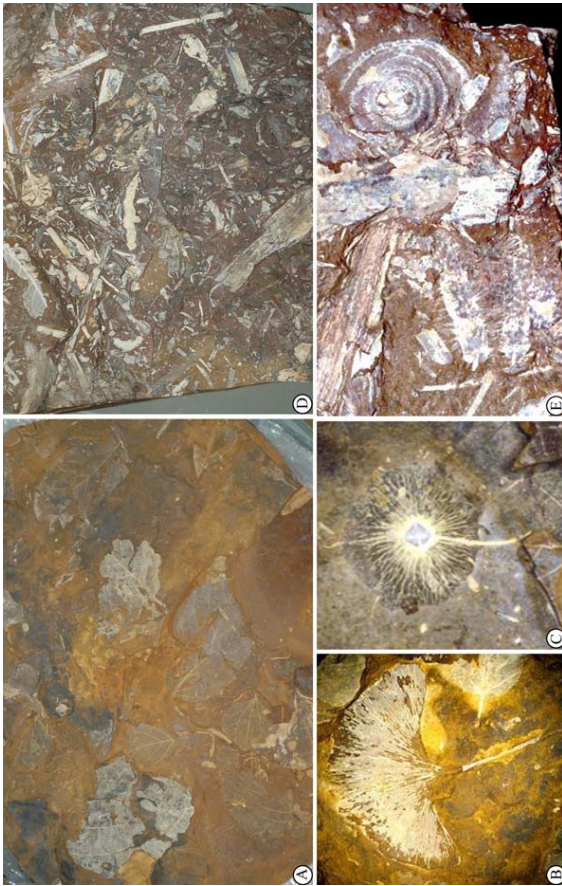


Figure 8. Comparison of Almont (A-C) and Beicegel Creek (D-E) matrices showing the low energy system of Almont and the higher energy system of Beicegel Creek. In Almont matrix, note the fine-grained particles and the large, relatively intact leaves (A). A *Ginkgo* leaf, a common fossil at Almont that is prized for its preservation by collectors (B), and *Cyclocarya brownii* (C) showing the overall morphology and little destruction of the wing. The Beicegel Creek matrix contains highly fragmented plant debris including stems, leaves, cones, and fruits (D). Note Taxodiaceous cone at top (D). A close up of Beicegel Creek material showing monocot rhizome at left with attached roots and leafy bud at right (E).



Chapter 3

RESULTS

Fossil fruits of *Cyclocarya brownii* are common components of both the Almont and Beicegel Creek floras. Over 200 individual fruits were studied, with 101 measured and around 20 studied in detail (Appendix A). Fruits are found on fractured surfaces of the rock matrix at both localities, and are also known preserved in section. The best-preserved specimens showing external morphology occur at Almont, and are similar to those previously described by Manchester and Dilcher (1982), also from this same site. These fruits are found as both silicified nutlets (Figs. 11a-g) and as sandstone casts (Figs. 11g-h). They are most often preserved vertically flattened on the plane of deposition, and usually show a well preserved nutlet surrounded by complete to nearly complete wings. For the first time, infructescences with 23 attached fruits have been discovered at Almont. (Figs. 9a-c).

In contrast to the Almont fruits, those at Beicegel Creek tend not to be flattened parallel to the bedding plane; instead there is no particular orientation to their occurrence in the matrix (Figs. 11a-g; 9a-c; 8d-e). Those found in fractured surface view have well preserved nutlets like those of Almont specimens, but in general, they have less complete wings. Other specimens are found embedded completely within the rock matrix. These show, for the first time, cellular detail of the fruit wall (Figs. 12a-h). Additionally, two specimens from Beicegel Creek found with anatomical preservation are of winged fruits with structures bearing

pollen attached to the fruit near its equator and extending upward (Figs. 14a-f; 15a-f; 16a-h).

Infructescences— One part-counterpart specimen and two individual infructescences are known from the Almont site (Figs. 9a-c; 10a-d).

Infructescences are 13 cm long, robust, and bear up to 23 pedicellate fruits. The infructescence axis (or peduncle) is up to 15 mm thick. Individual fruits are attached to the peduncle by elongate pedicels up to 25 mm long x 3 mm wide. Whereas some fruits are found in attachment to the axis, others not showing actual attachment are oriented as they would have been in life. Still others have pedicels oriented at other angles (Figs. 9a-c; 10a-d). It may be that some of these belong to other infructescences, and that some are isolated fruits. Another possibility is that some fruits were simply pushed at an angle from their original position during preservation, as their attachment is helical around the infructescence peduncle in three dimensions, rather than planar.

In one specimen in particular, only a few fruits are preserved in attachment to the peduncle, however the bases of 12 pedicels remain intact on the axis, demonstrating the original orientation of the fruits (Figs. 9b; 10a-b). Fruits attached to the infructescence are of fairly uniform size, and similar to those found individually (ca 27.3 mm in diameter). They were apparently mature fruits, with little evidence of immature or aborted fruits.

External morphological features of fruits — The majority of the fruits are preserved with the wing flattened in the vertical plane and completely surrounding the nutlet (Figs. 11a-c). However, some are found laterally compressed (Figs. 11d; 13a,e). Orientation of the fruit (i.e., whether it is being viewed from the top or the bottom) can be determined by details of the nutlet surface and attachment of the pedicel: viewed from the top the wing is viewed as lying over the pedicel. This is evident by observing the surface of the wing. The veins of the wing are continuous from the edge of the nutlet to the edge of the wing, and the pedicel is then observed beyond the margin of the wing. If the positioning of the pedicel is over the wing, there is a distinct disruption of the vein patterns of the wing. This is because the pedicel is lying on top of the wing and thus the fruit is being viewed from the bottom. By observing the relationship between the wing and the pedicel, it is very easy to orient the fruit and determine whether the apex or base of the nutlet (and consequently the entire winged fruit) is facing upward (Figs. 11a-c; 9a-c; 10a,c).

Fruits are 32 mm in diameter on average (20-48 mm, n=101) and consist of a central disk containing a small nutlet 3-6 mm in diameter (ave= 4.5 mm, n=101), surrounded by a circular wing with a width of 7 to 18 mm (ave=11.4, n=101). The nutlet of *C. brownii* is pyramidal with a complete secondary septum at the base. In cross section, these nutlets have a diamond shape (Figs. 11a-c, g-h), and longitudinally they are triangular at the top with a convex bottom (Figs. 11d; 13a-b, d-e). Two stelar arms were illustrated by Manchester and Dilcher

(1982, figs. 17, 18) at the apex of *C. brownii*, no further specimens of this structure have been found.

A circular wing of fairly even thickness surrounds fruits. Whereas most of the fruit wings have a smooth margin, some specimens have a more undulate or asymmetrically shaped outline (Figs. 11a-c). The wing of *C. brownii* is highly vascularized, with veins originating at the edge of the nutlet and continuing out to the margin of the wing (Figs. 11a-c). These veins both bifurcate and anastomose between the outer margin of the nutlet and outer edge of the wing (Figs. 11a-c). Four of the veins are considerably thicker: two are perpendicular and two parallel to the main axis of the fruit, separated by the nutlet in the center. The orientation of these thicker veins results in a prominent cross shape (Figs. 11a, c, g).

Fruit anatomy— Many fruits of both localities have internal anatomical preservation. Those from Almont have been studied with wafered serial sections to reveal the basic organization and sometimes detailed cellular structure, while those from Beicegel Creek show excellent cellular preservation comparable to that seen in coal balls or silicifications (e.g., Princeton Chert).

The center of the nutlet contains the embryo cavity, which is divided by a primary septum, with a partial secondary septum occurring at right angles to the primary septum. In transverse serial sections from 2 - 4 locules are visible, depending on the plane of section (Fig. 13b).

The fruit wall is made up of six distinctive layers of cells (Figs. 12a-f). Immediately lining the locules is a layer 3-4 cells thick of tangentially elongate sclereids $25\text{ }\mu\text{m} \times 10\text{ }\mu\text{m}$ (Figs. 12a-c, e). Thinner-walled, large isodiametric idioblast cells $10\text{ }\mu\text{m}$ in diam are also found scattered within this layer (Figs. 12a-c). To the outside is a second layer is 4-5 cells thick and consists of isodiametric sclereids that are relatively small in comparison to the surrounding cells. The thickness of this layer varies between specimens and regions on the same specimen from $40\text{ }\mu\text{m}$, to over $100\text{ }\mu\text{m}$. This layer grades into a third region, which makes up the bulk of the nutlet wall. In the third layer cells are larger, thicker-walled sclereids $8\text{-}10\text{ }\mu\text{m} \times 9\text{-}11\text{ }\mu\text{m}$, with deeply undulating margins that make up the layer completely. Idioblast cells are lacking. The fourth layer is 1-3 cells thick depending on the section of the fruit wall being observed and have palisade-shaped sclereids $10\text{ }\mu\text{m} \times 5\text{ }\mu\text{m}$. The fourth layer is bordered by a fifth region comprising a single layer of relatively large idioblast cells $10\text{ }\mu\text{m}$ in diam that contain crystal-like structures (Figs. 12a-b, e-f). These idioblast cells are not as thick-walled as the other cells located adjacent to them. Additional idioblasts are scattered throughout the sclereid layers, as well as numerous tannin cells (Figs. 12a-f).

Finally, to the outside of the idioblast cells is the sixth layer, which is about 10 cells thick, composed of small, very dark, tangentially elongated cells that are $10\text{ }\mu\text{m} \times 3\text{-}4\text{ }\mu\text{m}$. These cells are difficult to distinguish individually, possibly because this is the outer layer in direct contact with the environment

during the fossilization process and was damaged or partially distorted during fossilization. Neither epidermis nor cuticles are preserved.

Wing morphology, attachment and anatomy— The wing is attached to the base of the nutlet and encases the lower hemisphere (Figs. 13b-d). It wraps from the base to the equator of the nutlet before it separates and forms the wing in the same plane of the equator. The base of the nutlet where the wing is attached is rounded whereas the apex hemisphere of the nutlet is pyramidal as described previously (Manchester and Dilcher, 1982). The wing contains many veins that bifurcate and anastomose along their route from the edge of the nutlet to the margin of the wing (Fig. 13a; 11a-h). The wing is circular and completely surrounds the nutlet symmetrically. There is no differential thickening of the wing at any point, and the only obvious difference in the wing is the 4 thicker veins that form the previously described cross shape (Figs. 11a, c, g). The wings range from 7- 18 mm in radius with an average radius of 11 mm (n=101). The radius of the wing is also referred to as its width and is measured from the edge of the nutlet to the margin of the wing. Since the wings are radially symmetric, they are uniform in radius from any point on the nutlet. This is a generalized statement, as there are slight differences in the radius because of taphonomic and developmental biases (Figs. 11a-c).

Fruits with attached pollen-bearing structures— Two fruit specimens are distinct in having pollen-bearing structures attached to them (Figs. 14a-f; 15a-f; 16a-h). The structures are attached laterally on either side, at a position at the level where the nutlet begins to narrow into its apical point (Figs. 16a-h). The first specimen is a fruit sectioned longitudinally from the center of the fruit tangentially outward. In midsection two elongate structures extend around 1 mm vertically from their points of attachment (Fig. 16a). These elongate structures then branch distally, resulting in a thicker portion to the inside and a thinner portion to the outside (Figs. 16a-h). The outer portion extends up and curves inward toward the fruit apex. In the area between these two portions are scattered juglandaceous pollen grains (Figs. 16a-h). Following the structures through the successive peels tangentially, the attachment is no longer evident, but pollen sacs with prominent palisade walls appear (Fig. 16f). In the most tangential location there are several pollen sacs present with in situ juglandaceous pollen that is similar to the pollen found in extant *Cyclocarya paliurus* (Fig. 16f). Some of the successive peels also contain tissue oriented above the apex of the nutlet (Figs. 16f-g). While this tissue is not connected to the nutlet, it is in the position that the commissural stigma would be located on the extant form of *Cyclocarya*

A second specimen, also sectioned longitudinally from the center like the first contains a larger pollen structure that is curved around the apex of the nutlet (Figs. 14a-f). The structure is attached at the same location on the nutlet as the first and contains 2 well preserved and 5 poorly preserved pollen sacs oriented

around a central axis (Figs. 15a-f). Wrapping around the pollen sacs are leafy structures, which encase the sacs in whorls. The leafy tissue surrounds the pollen sacs in an umbrella-like shape (Figs. 15a-f). The pollen in the second specimen is also assignable to *Cyclocarya* and the general morphology of the pollen when viewed through light microscopy (Figs. 19d, f-g).

The pollen within these structures varies from triangular to circular in outline, as in extant *Cyclocarya* (Fig. 19d, f-g). It is 3-4 porate (with 4 porate being the more common type), and has prominent folds that resemble arci. However, these folds are irregular in orientation and likely due to preservation (Fig. 19d, f-g). The exine appears psilate under light microscopy; however, jugandaceous pollen typically has tiny spinules only visible with SEM (Zetter et al., in press). The pollen appears mature; with the grains separate from one another and very little of the pollen sac tissue is preserved. (Figs. 15a-f; 16a-h; 19f-g).

Figure 9. Two infructescences from the Almont locality; 2 part-counterpart specimens (A, C) and a single specimen (B). A, UWSP 4372b; B, UWSP 1987; C, UWSP 43272a; mm scale at top right (A), bottom right (B), and side (C). Scale=1 cm.

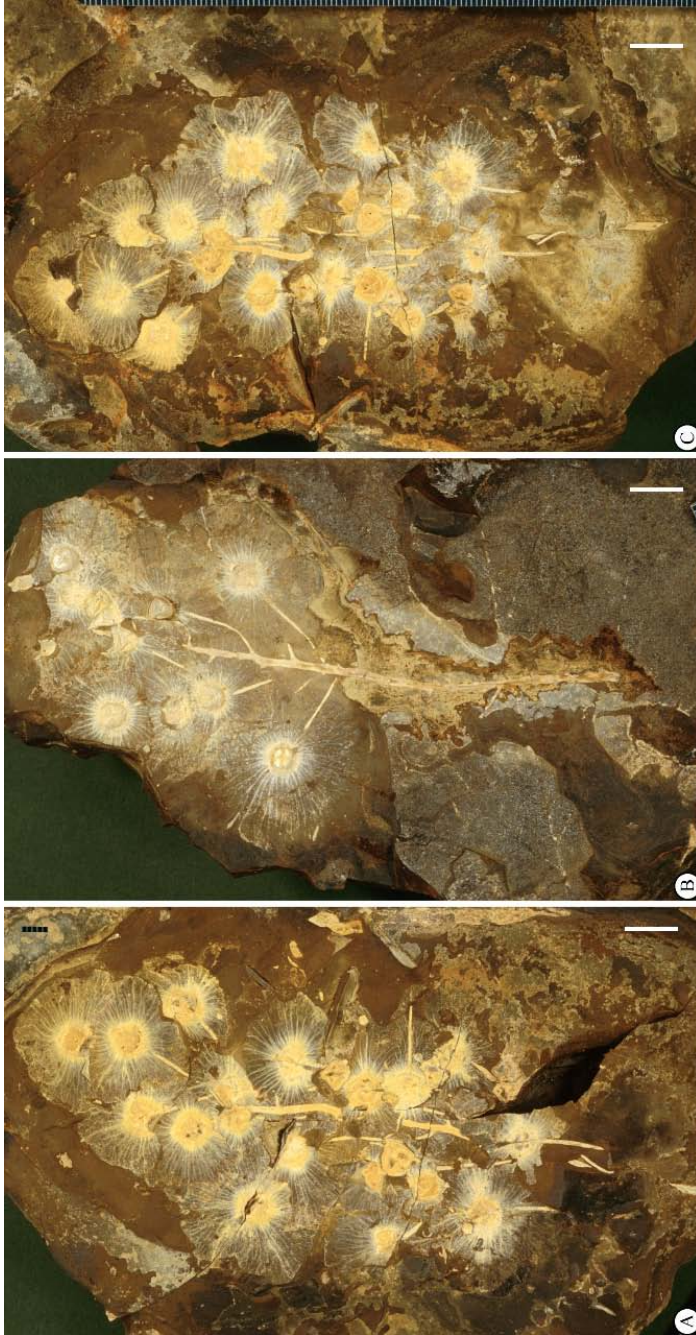


Figure 10. Infructescences and line diagrams showing fruiting axis with attached fruits. The numbers indicate positions of attached fruit pedicels or fruits (A-B).

The line diagram is a higher magnification of the fruit axis (B), UWSP 1987.

Infructescence with individual fruits labeled (C-D). This specimen has fruits indicated by blue dots, pedicels by pink lines, and the main axis by green lines,

UWSP 4372a. Scale=1cm.

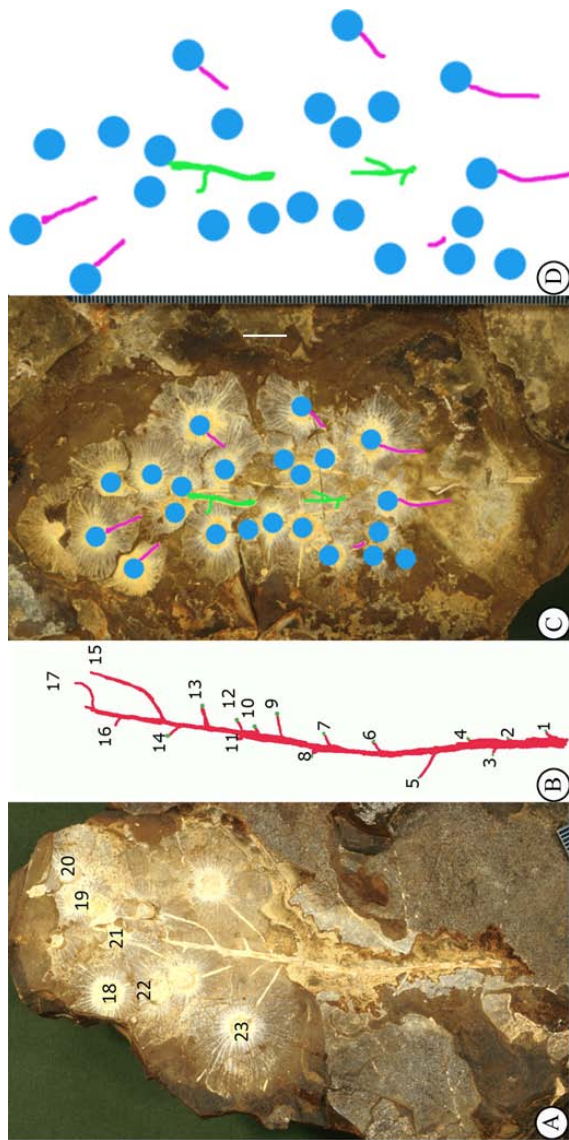


Figure 11. Individual fruits of *Cyclocarya brownii* showing the variation in the margin of the wing (A-C); a longitudinal section of the fruit (D); a single specimen that has two nutlets surrounded by a single wing (E-F); a block with multiple fruits (G); and a cast of the nutlet where the nutlet has been removed and the imprint is left (H). A, ASU Cyclo1; B, ASU Cyclo 2; C, ASU Cyclo 3; D, UWSP 3569; E-F, UWSP 4622; G, ASU Cyclo 4; H, ASU Cyclo 5.

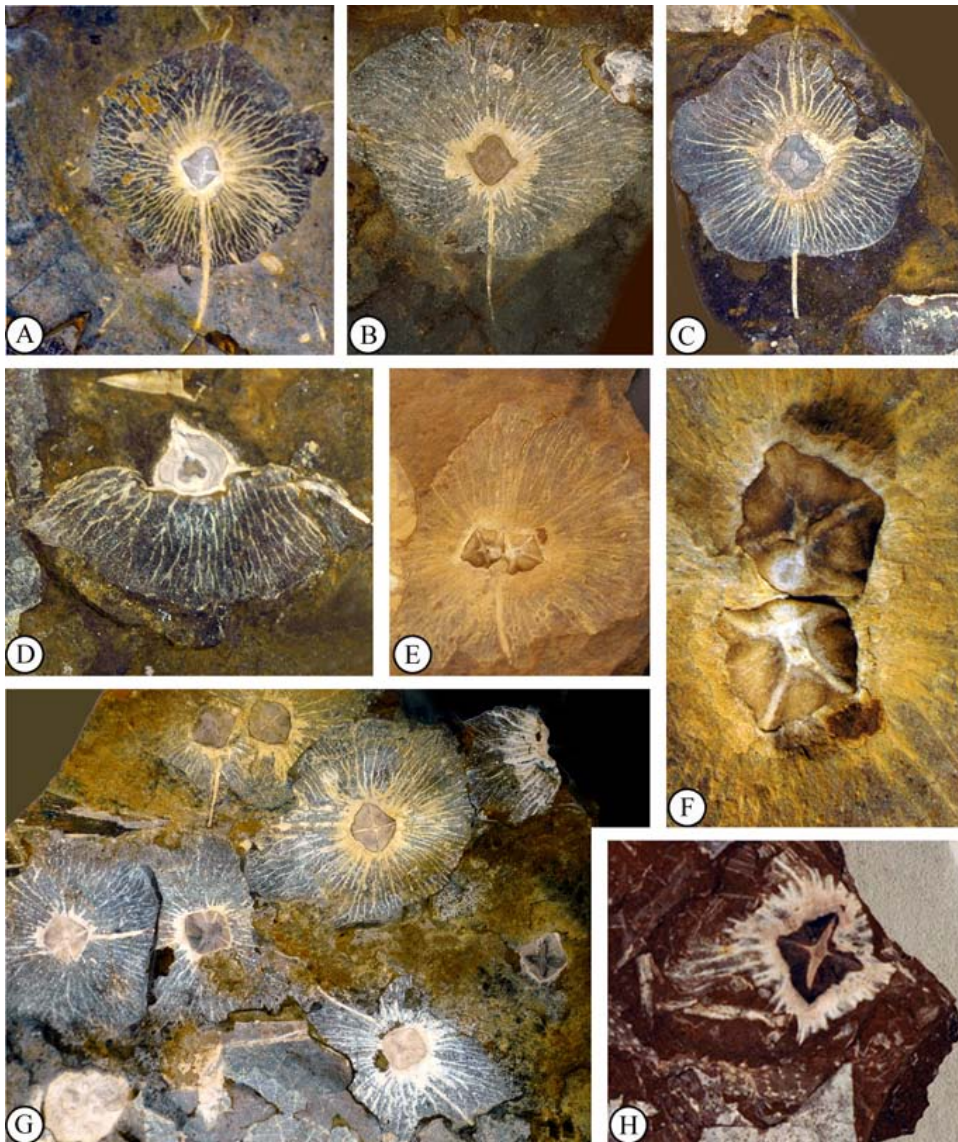


Figure 12. Light micrographs of peels from the Beicegel Creek material. Six distinctive cell layers can be seen in the fruit wall (A-F). The innermost layer (A-C) containing tangentially elongated cells lines the embryo cavity. A second layer contains isodiametric sclereid cells with thick walls (A-B, D) that grades into a third layer of larger, sinuous sclereids (A-B, D). The fourth layer contains palisade shaped sclereid cells (A-B, E), which are surrounded by a fifth layer of thin walled idioblast cells containing crystals (A-B, E-F). The sixth and outer layer contains tangentially elongated, very dark cells (A-B, F). The wing tissue is made of thin walled cells with large veins (G). Some of the sclereids can look like fibers due to development in the apex of the fruit (H).

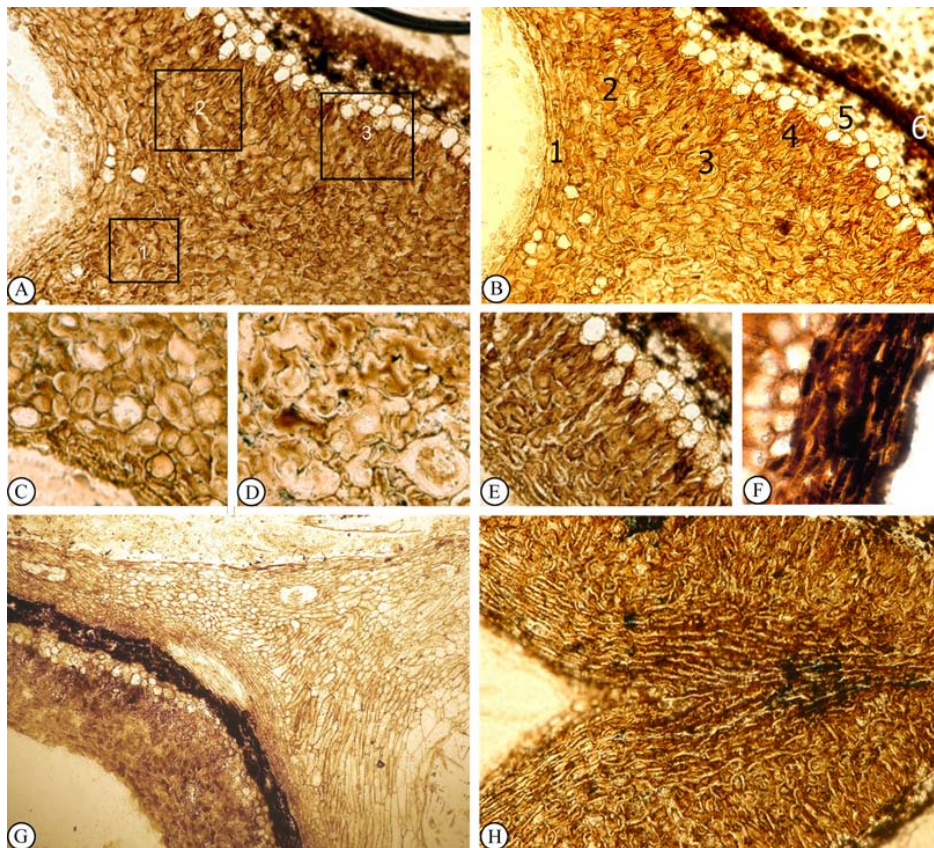


Figure 13. The attachment of the wing to the nutlet. The original attachment was described as basal based on a fractured fruit from Almont (A, E) but the new material from Beicegel Creek shows the wing leaving the nutlet from a more equatorial position (B-C) and cupping the base of the nutlet. Some of the new Almont material, when wafered with a saw, shows the same orientation as the Beicegel Creek peels (D). Scale=2mm.

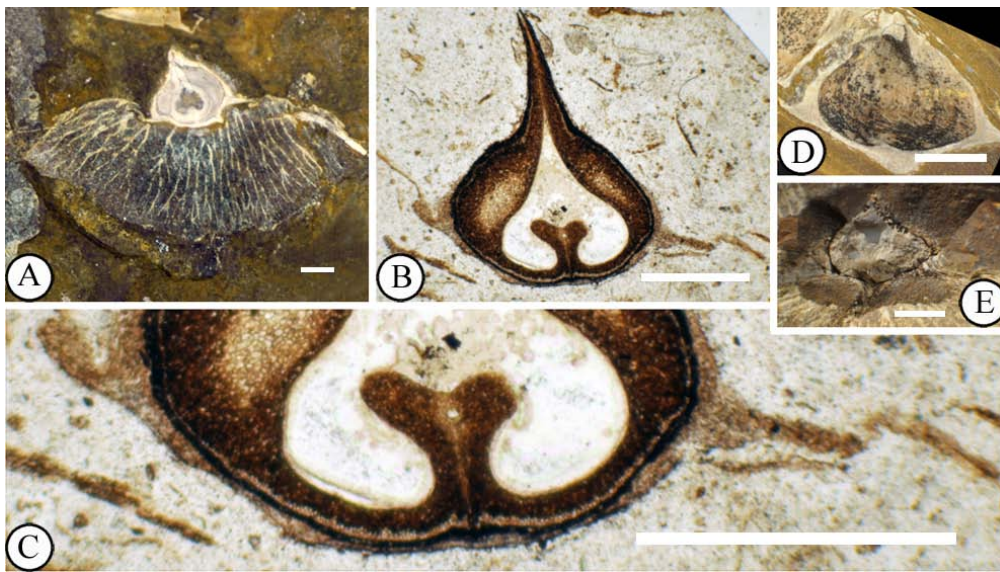


Figure 14. A fruit with attached pollen structures (A-F). The fruit is sectioned in an oblique longitudinal view, going from a near medial section (A) to a more tangential section (B-F). Pollen bearing structures are attached at upper left and arch over the apex of the fruit. ST1, A=#6; B=#5; C=#4; D=#3; E=#2; F=#1. Scale=2mm.



Figure 15. Detail of figure 14 showing the pollen structure (A-F). The structure contains 2 complete pollen sacs with in situ pollen, and multiple ruptured pollen sacs. ST1, A=#1; B=#2, C=#3; D=#4; E=#5; F=#6. Scale=1mm.

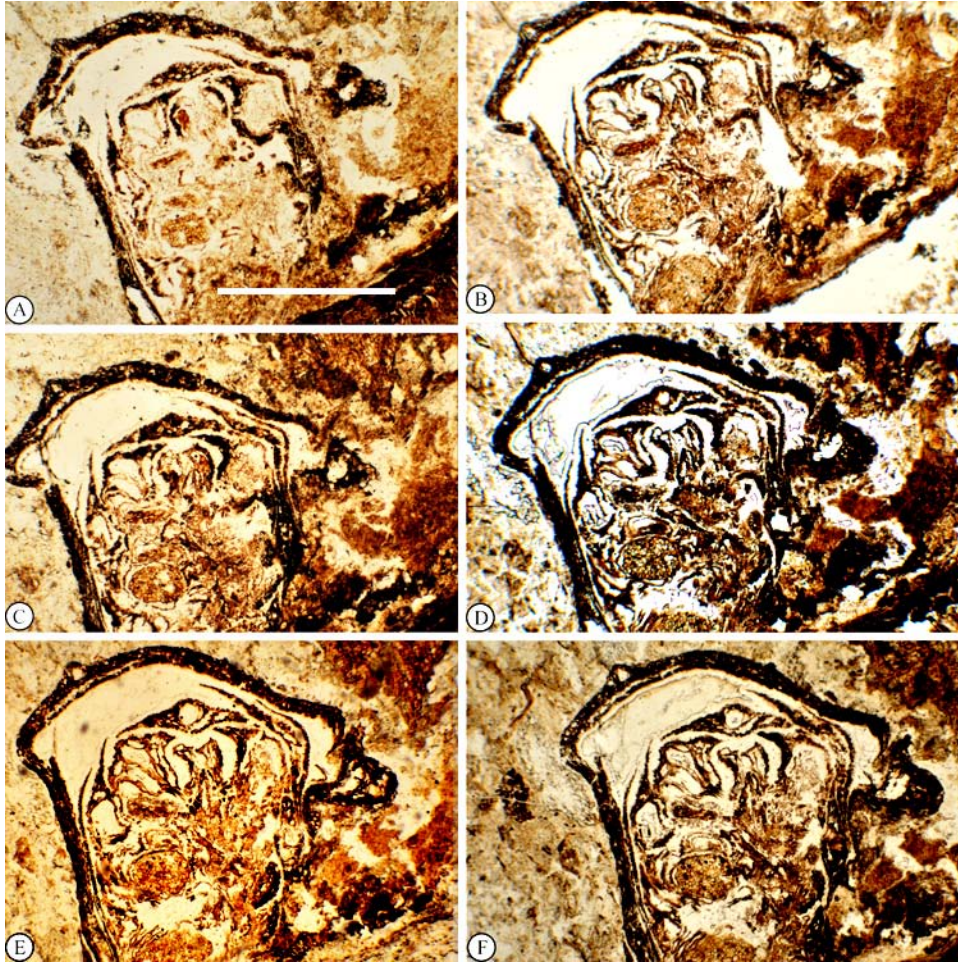


Figure 16. Serial tangential sections through the apex of fruit with pollen-bearing structures. Section A is the most median and H the most tangential. A and B show the attachment of these structures to the fruit, H shows the basal part of the style. All sections show fragments of pollen sacs containing mature pollen. KB 12, A, #30, B, #22, C, #17, D#7, E #5, F#4, G#2, H #1. Scale=1mm.

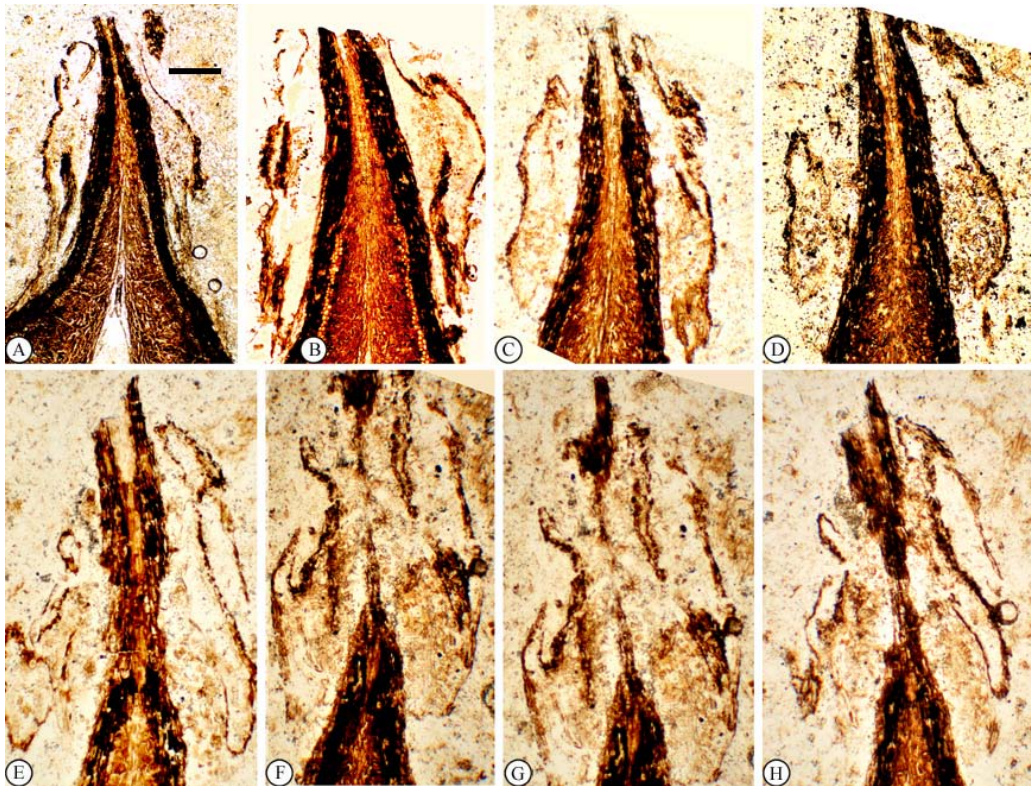


Figure 17. *Cyclocarya paliurus* infructescences (A-B) and line diagrams showing the attachment of the fruits to *Cyclocarya paliurus* (C) and *Cyclocarya brownii* (D). Extant *Cyclocarya* is a spike (A-C), whereas the fossil form has pedicellate fruits attached to a main axis (D). The pedicels are indicated by a pink line, the main axis is a green line, and the fruits are labeled with blue circles (C-D). A is from www.ruhr-bochum.de; B is from www.plantsystematics.org; accessed 1 October 2010.

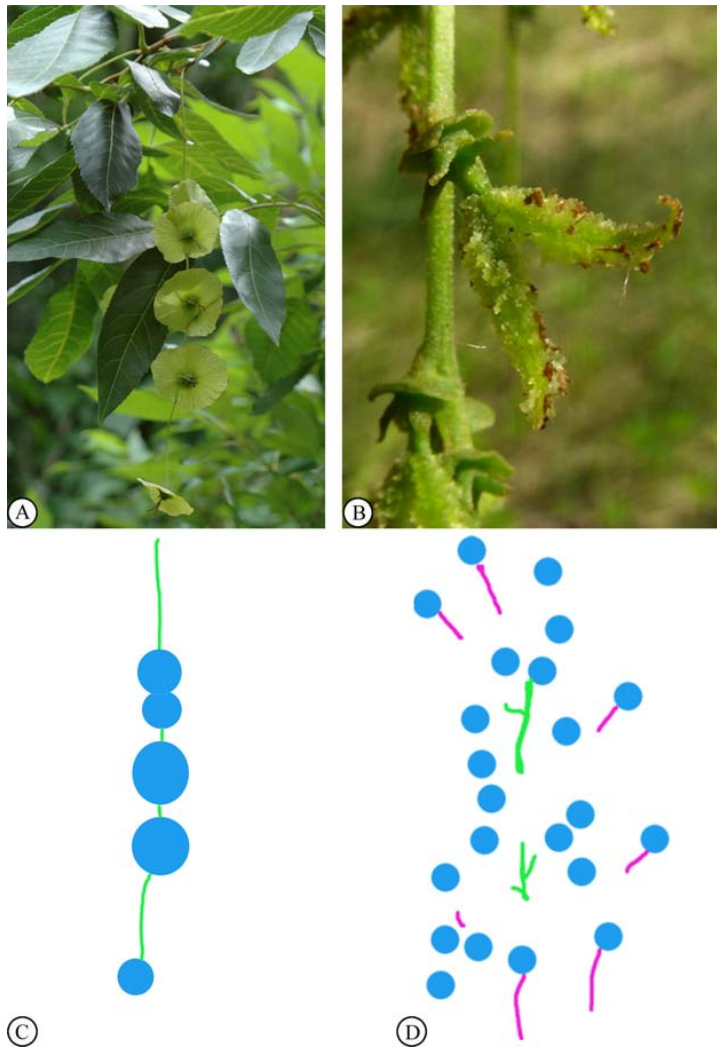


Figure 18. An associated pollen catkin from the Almont locality (A, C) compared to extant *Cyclocarya paliurus* (B, D). B is from www.ruhr-bochum.ed; accessed 1 October 2010.

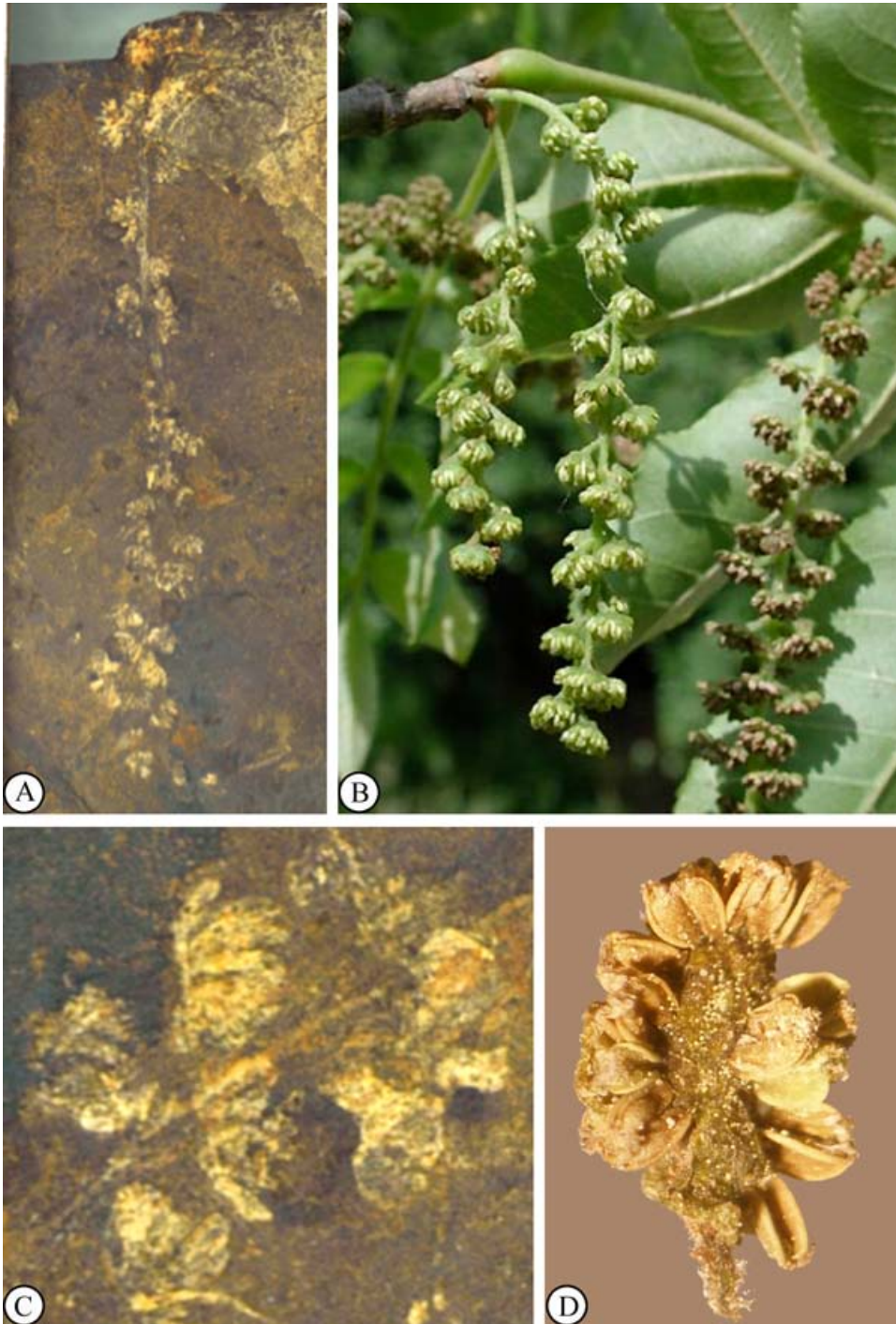
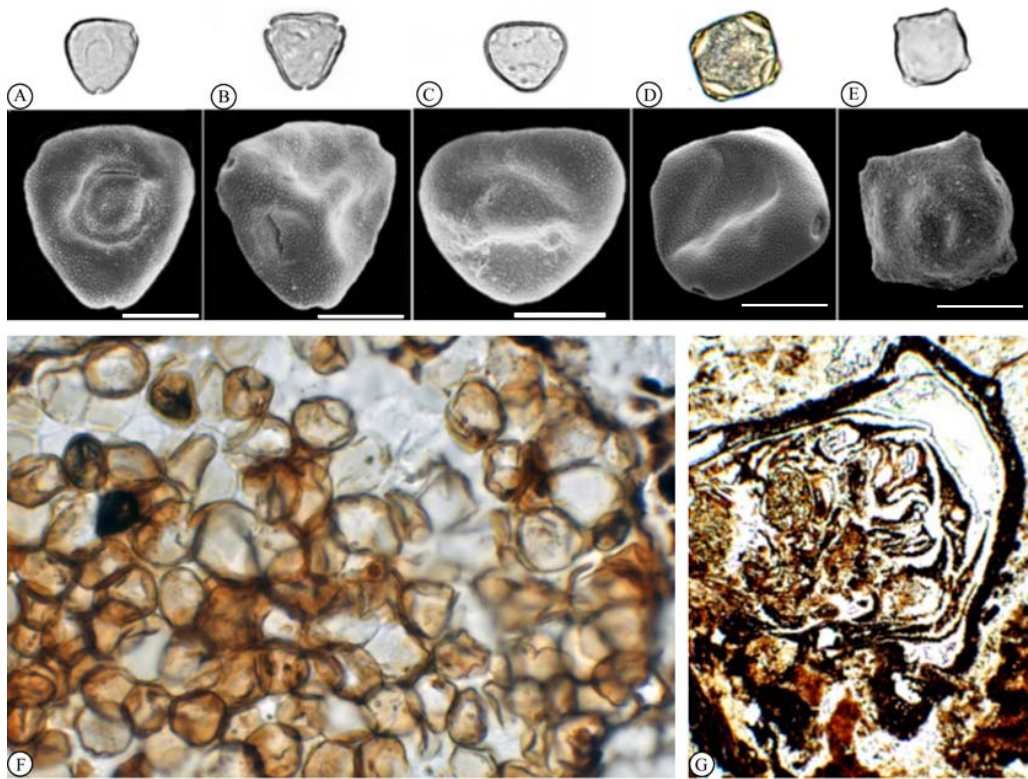


Figure 19. Juglandaceous pollen in the Almont matrix in LM and SEM (A-C, E) with *Cyclocarya paliurus* pollen for comparison (D). A pollen structure found attached to a *Cyclocarya brownii* fruit (G) with in situ pollen (F) comparable to the extant form. *Momipites annulus* (A); *M. triorbiculatus* (B); *Caryapollinites imparalis* (C); *Cyclocarya paliurus* (D); *Polyatriopollinites* sp. (E); ST1 #3 (F-G). Scale=10 μ m.



Chapter 4

SYSTEMATICS

Cyclocarya —Family— Juglandaceae

Subfamily — Juglandoideae

Tribe — Juglandae Manning 1978

Genus— *Cyclocarya* Iljinskaya 1953

Species— *Cyclocarya brownii* Manchester and Dilcher emend. Taylor

Pterocarya hispida Brown 1962, fruits only. p. 57, Pl. 68, fig. 12, 13.

Pterocarya hispida Brown, in Hickey 1977. p. 119, Pl. 15, fig. 9.

Cyclocarya brownii Manchester and Dilcher 1982, Fig. 1-5, 9-11, 15, 17-24, 28.

Cyclocarya brownii Manchester 1987, p. 93, Fig. 39 B-J.

Cyclocarya brownii Crane, Manchester and Dilcher 1990, Fig. 18.

This project has produced new character information for *Cyclocarya brownii*. The infructescences found at the Almont locality has provided not only the overall structure, but also the attachment of the fruits to the axis. The infructescences are large and robust, up to 13 cm in length with as many as 23 fruits attached on pedicels up to 25 mm long. The Beicegel Creek material, showing the internal anatomy of the fruit, has provided evidence for the connection of the wing to the nutlet. The wing wraps around the base of the nutlet, cupping it, and extends from an equatorial position. The fruit wall is made up of 6 distinctive cell layers and contains large, thick-walled sclereids as

well as large idioblasts scattered throughout. The combination of these new features added to the original description will aid in the identification of fossils that have questionable resemblances to *Cyclocarya* and aid in a better comparison to the extant species.

In the following section, the original diagnosis of *Cyclocarya brownii* by Manchester and Dilcher (1982) is presented, with newly recognized features indicated in boldface type.

Diagnosis — (as in Manchester and Dilcher 1982; new features bolded)-

Infructescence robust, peduncle 13 cm long x 1.5 cm wide, attached fruits up to 23; fruits pedicel late, pedicels up to 25 mm long x 3 mm wide, fruit a winged nutlet, 25-43 mm diam (avg. 32 mm); **wing surrounding lower hemisphere of nutlet**, flange-like, coriaceous, circular, wing margin smooth to irregular; veins of wing bifurcating and occasionally anastomosing; nutlet 3-6 mm diam; smooth-surfaced, pyramidal, diamond- shaped in cross section, triangular in longitudinal section, tapering apically; styler arms 2, diverging from nut apex.

Fruit wall 6-layered, innermost layer lining locules 3-4 cells thick, of tangentially elongate sclereids, second layer thinner-walled, large isodiametric idioblast cells, third layer of variable thickness, of isodiametric sclereids relatively small in comparison to surrounding cells, grading to larger, thicker-walled sclereids with deeply undulating margins, idioblasts lacking; fourth layer of palisade-shaped sclereids, fifth layer uniseriate, of relatively large idioblast cells containing crystal-like structures, additional

idioblasts scattered throughout sclereid layers, tannin cells numerous, sixth layer ca 10 cells thick, composed of small, very dark, tangentially elongated cells.

Type locality — NW ¼, Sec. 26, T.140N., R.86 W. , Morton County, North Dakota.

Stratigraphy — Late Paleocene, Fort Union Formation, Sentinel Butte Member, Tiffanian-3

Holotype — IU 15722-4031 (Fig. 1, 17, 18 in Manchester and Dilcher, 1982; Fig. 39F G, H in Manchester, 1987).

Paratypes — IU 15722-4032 (Figs. 2, 3 of Manchester and Dilcher, 1982; Fig. 39I in Manchester, 1987); IU 15722-4033 (Figs. 4, 5 of Manchester and Dilcher, 1982); IU 15722-4034 (Figs. 10, 11, 19-24, of Manchester and Dilcher, 1982); IU 15722-4035 (Fig. 11 of Manchester and Dilcher, 1982); IU 15722-4036 and IU 15722-4041; USNM 298816, Fig. 16 of Manchester and Dilcher, 1982); USNM 298817. IU 15722-4762, Fig. 39B in Manchester, 1987. **ST1 #1-30; KB12 #1-6; ASU Cyclo 1-6; UWSP 4372a; UWSP 4372b; UWSP 1987; UWSP 3569; UWSP 4622.**

Etymology — The specific epithet commemorates Roland W. Brown.

Deposition of specimens — IU specimens are housed in the Florida Museum of Natural History Collections; USNM specimens are housed at the National Museum of Natural History (Smithsonian Institution, Washington, DC). UWSP; ASU; PP; North Dakota Heritage Museum.

Chapter 5

DISCUSSION AND CONCLUSIONS

The fossil history of the Juglandaceae is among the longest and best known among extant families of angiosperms. While floral and fruit remains preserved as mesofossils referable to the order Juglandales first appear in the Late Cretaceous of eastern North America and Europe (Friis et al., 2004), with one possible exception (Crepet et al, 2004) generally they cannot be resolved at the level of family. Pollen with similarities to the Normapolles complex, also present from the Late Cretaceous into the Eocene, has been considered closely related to Juglandaceae. Megafossils of fruits that can confidently be placed in the family first occur in the early Paleocene of Far East Russia (Kodrul and Krassilov, 2007), with the late Paleocene of western North America serving as a nexus for diversification. Of these late Paleocene forms, the extinct genera *Polyptera* and *Cruciptera* Manchester, and the extant genus *Cyclocarya* are the first to occur (Manchester and Dilcher, 1982; Manos and Stone, 2004).

As early as the late Paleocene, three species of *Cyclocarya* are already present in western North America (Manchester and Dilcher, 1982). Of these, the best record is of *C. brownii*, the subject of the present study. The other two species, *C. coalmontensis* Manchester and Dilcher and *C. minuta* Manchester and Dilcher, are known only from compressions that offer less detailed information. Other genera of both subfamilies Juglandoideae and Engelhardioidae are known from the Eocene on in western North America with younger occurrences present

in Europe and Asia (Manchester, 1994, 1999; Manos et al., 2007). While *Juglans* and *Carya* remain present in North America, the current distribution of many of these taxa in Asia, including *Cyclocarya*, suggests that it is a refugia for the genera that originated in North America and spread across Europe to Asia (Manchester, 1999).

New information on *Cyclocarya brownii*— Since its first description based on 17 specimens (Manchester and Dilcher, 1982), a much larger number of *Cyclocarya brownii* specimens have become available for study from both the original Almont site (Manchester, 1987; Crane et al., 1990) and the more recently discovered Beicegel Creek locality (Manchester et al., 2004). Based on these additional specimens, this study provides new information about: 1) the attachment of fruits to the infructescence axis, 2) the anatomical structure of the fruit wall, 3) a new interpretation of wing structure and attachment, and 4) the presence in some specimens of pollen structures containing mature pollen attached to the fruit. Additionally documented are 5) associated pollen catkins with the structure consistent with that of extant *Cyclocarya*, and 6) several types of dispersed juglandaceous pollen grains, some of which are similar to those found in the pollen structures attached to fruits, and to extant *Cyclocarya* pollen. Isolated leaflets with suggested juglandaceous affinities have been reported from the Almont site (Crane et al., 1990), however, they are quite rare and complete

compound leaves are insufficiently known for detailed comparison, and so are not discussed in this study.

The most striking newly found *Cyclocarya brownii* fossils are the infructescences from the original Almont locality (Figs. 9a-c). This is the first time that the fossil fruits of *Cyclocarya* are found attached to an axis and therefore can be directly compared to the living species. There are substantial differences between the late Paleocene infructescence and that of extant *Cyclocarya paliurus* (Figs. 10a-d; 17a-d). Extant *Cyclocarya paliurus* has a long, pendulous inflorescence, a spike, with up to 10 attached flowers, and later, fruits. The fruits are borne directly on the fruiting axis, rarely with very short pedicels (up to 0.5 mm long), more commonly with completely sessile fruits (Fig. 14). The fruiting spike is elongate, pendulous, and glabrous and ranges from 25-30 cm in length.

In contrast, the infructescence of *Cyclocarya brownii* is quite different from its extant relative. The infructescence, and presumably the inflorescence is a raceme, with pedicillate fruits along the axis. The pedicels are relatively long, up to 25 mm. One of the infructescences contains 23 fruits associated with it, with three fruits in attachment and the others in the original position in relationship to the fruiting axis. A second specimen also has three fruits attached and although fewer fruits are seen in association, the main fruiting axis has eleven points of pedicel attachment. The fruiting axis of *C. brownii* is much more robust than its extant relative (~2 mm wide in comparison to 0.5-1 mm in *C. paliurus*). However, it also appears to be terminal on the branch (Fig. 17a). The fruits are

also organized in a more three-dimensional structure in the fossil species, in contrast to a planar infructescence in the extant form. This is evident by the attachments on the axis, and by orienting the fruits based on the position of the pedicel to the wing. By orienting the fruits to the living position on the axis, a densely packed helical raceme can be imagined (Figs. 9a-c; 10a-d; 17a-d). There is no evidence that panicles were formed, because the pedicels attached to the axis lack any structures that indicate branching and are the same thickness from the axis to the base of the fruit.

The fruits all are relatively the same size, with no indication of underdeveloped or juvenile fruits (Figs. 9a-c; 10a-d; 17a-d). Typical racemes in extant *Cyclocarya* develop from the base outward to the apex, with flowers and thus fruits becoming mature at the base first and the apex last (Manning, 1938). Since there is no evidence on any of the infructescences (or isolated fruits for that matter) indicating a juvenile or underdeveloped fruit, the developmental order cannot be determined in the fossil infructescence. It is assumed that once the infructescence developed from the racemous infructescence the basal fruits were robust enough to last through the developmental period until all fruits are fully mature and then disperse at the same time. A similar situation is found in *Corylopsis* Siebold and Zuccarini sp. (Hamamelidaceae) and other extant members of the Hamamelidaceae where the mature infructescences contain fruits of relatively similar size so the fruits look the same from the base to the axis (John C. Benedict 2010, personal communication). This evidence shows that the

Cyclocarya infructescences found in Almont are pre-dispersal, but post-development.

Specimens from Beicegel Creek allow for a detailed comparison of the anatomical structure of fruit wall with the extant *C. paliurus* and other juglandaceous fruits. As in all fruits of Juglandaceae, the fruit wall is highly sclerified, resulting in a hard shell for the nut, or nutlet. Zonation in the *C. brownii* is complex, with around 6 distinct layers. Tangentially elongate cells circle the embryo cavity, and larger, thick-walled isodiametric sclereids comprise the bulk of the fruit wall. Idioblasts occur both within some layers and in a ring in the outer fruit wall.

Manchester (1987) noted that variation in the mature fruit walls (nutshells) of juglandaceous nuts and nutlets tends to fall along subfamily lines. Members of Engelhardiidae have nutshells composed of elongate fibers, while those of Juglandoideae are made up of “isodiametric” sclereids (Manchester, 1987; Manos and Stone, 2001; Elliott et al., 2006). *Beardia*, an Eocene fruit from Vancouver Island, BC, was compared to Engelhardiidae on the basis of the elongate, thick walled fibers that make up the fruit wall. This feature can be found developmentally in *Cyclocarya brownii* as the sclereids will flatten and elongate in the apex of the nutlet due to decreased room for expansion (Fig. 12f). However, this fruit demonstrates a characteristic pattern of large idioblasts occurring toward the outer nutshell, a feature that was previously unrecognized

among Juglandaceae. Based on a mosaic of characters, *Beardia* was interpreted as transitional between the two modern subfamilies.

In contrast to both *Beardia* and previous descriptions of juglandaceous fruit wall (Manchester, 1987; Manos and Stone, 2001; Elliot et al, 2006), *Cyclocarya* has several distinctive features. The nutshell is made up of sclereids. However, they are not uniformly isodiametric, instead varying from rectangular, to sinuous, to palisade-like. They also vary in relation to one another, such that the nutshell has a complex organization. Large, thin-walled idioblasts similar to those of *Beardia* are distributed both in a single band, but also occur dispersed throughout the fruit wall, in the different sclereid layers. Moreover, many idioblasts in *Cyclocarya* have angular crystals within them, a feature not previously noted.

The early stages of fruit wall development in Juglandaceae have been described for *Juglans* and *Carya* (Roth, 1977). However, development has not been characterized for other genera in detail, and comparison of young fruits with mature ones is made difficult by the problems in softening the hard sclerenchymatous shells of mature nuts and nutlets.

Comparison of fossil *Cyclocarya* nutshells with those of extant *Cyclocarya* fruit walls was done in a preliminary way, by wafering the extant specimens on a trim saw and studying them under a compound microscope with reflected light. Good anatomical sections were difficult to obtain, using several different standard methods (Sherwin Carlquist, personal communication, 2007). What was observable from the extant sections is that they too are made up of a

complex combination of sclereids of different shapes, and that idoblasts make up an outer ring on the fruit wall, as well as being scattered throughout (not figured). These results suggest that this character may be of further taxonomic value.

Several authors have discussed the origin of the wing in *Cyclocarya*, largely in the context of the biwinged *Pterocarya* to which it was originally recognized as *Pterocarya paliurus*. Initially it was thought to be a fusion of two wings, such as those in *Pterocarya*, which originate from the bracteoles (Manos and Stone, 2001, 2007). While Iljinskaya (1953) proposed *Cyclocarya* as a genus distinct from *Pterocarya*, others retained this form in *Pterocarya* (Manning, 1978), and generally did not recognize the new genus until the 1990s (Manos and Stone, 2001). Other fruits in Juglandoideae lack wings, however fruits of the other subfamily Englehardioidae have small nutlets with a variable number of wings, but there seems to be no homology between wing origin in the two subfamilies (Kodrul and Krassilov, 2007).

Manchester and Dilcher (1982), studying several species of fossil *Cyclocarya*, interpreted the wing of the fossil forms of *Cyclocarya* and *Polyptera* as all having a basal attachment. This analysis was based on laterally compressed fossils. In contrast, extant *Cyclocarya* has a wing that expands from the nutlet at the equator. With the study of anatomically preserved specimens from Beicegel Creek, it is clear that the wing of *C. brownii* is oriented in the same manner as the extant fruit, wrapping around the base of the fruit and extending equatorially

(Figs. 13b-c). Study of the extant fruit anatomy of *C. paliurus* confirms this similarity.

One surprising discovery is two permineralized fruits that have pollen-bearing structures attached directly to them, a feature uncharacteristic of the modern genus (Manos and Stone, 2001, Manos et al., 2007). The structures are inserted laterally at the level where the fruit begins to taper distally to its tip, and in the position where stamens or staminodes would most likely occur. Of the two specimens in which these structures are found, the first one shows their general positioning in relation to the fruit, but lacks details of the stamens. The second specimen shows both anthers with intact pollen sacs full of juglandaceous pollen, as well as dehiscent anthers. Although the pollen from these anthers have not yet been viewed using an SEM, they have several features that are associated with juglandaceous pollen. The pollen grains are round, 3 to more commonly 4 porate, with pores on the equator of the grain. There are no obvious ultrastructure features when viewed with light microscopy. The Juglandaceae have microechinate on the surface of the pollen grain, a feature only observable under SEM.

Even though all extant Juglandaceae, with the exception of *Platycarya*, have unisexual fruits, there are occasional reports of rudimentary stamens or staminodes occurring in comparable regions on extant *Cyclocarya* fruits (Manning, 1938; Manos and Stone, 2001). Additionally, the live material of *Cyclocarya paliurus* that was studied comparatively typically shows four small

pointed structures in this same position. Moreover, wafered sections of extant fruits demonstrate that in longitudinal section these structures are markedly similar to those seen in the fossil. Whereas some authors have interpreted these structures as calyx lobes, they clearly appear to be in the correct morphological position and orientation to be considered rudimentary stamens, as noted by Iljinksaya (1953). Manchester and Dilcher (1982) noted the presence of a two-armed stigma and illustrate these arms as small structures parallel to one another (Figs. 17, 18 of Manchester and Dilcher, 1982). However, in comparison with the structures seen in these fossils and with extant *Cyclocarya* fruits, the specimens illustrated by them may be comparable to the present structures, rather than to a bifid stigma. There is little to no evidence of the large prominent bifid branching stigmas characteristic of extant *Cyclocarya* and juglandaceous genera as a whole (Manning, 1938).

Whereas extant Juglandaceae are almost all unisexual (except for *Platycarya*) the closest sister family Rhoipteleaceae has bisexual flowers. Manning (1938) theorized that the ancestor of Juglandaceae was bisexual, and provided a hypothetical transformational series by which extant Juglandaceae might occur. This series was believed to have begun with a pre-juglandaceous ancestor and progress to the modern, highly reduced form of *Carya*. *Platycarya* was determined by Manning (1938) to be a primitive form of the family since it is the only member with bisexual flowers.

The two fruit specimens in the current study showing attached pollen structures on the fruit could be interpreted in several ways. It is tempting to suggest that their presence in Paleocene fossils support Manning's (1938) hypothetical series. *Cyclocarya* is one of the longest-lived genera of the Juglandaceae and it is plausible that the late Paleocene species could have a bisexual flower unlike the unisexual flower that we see in *Cyclocarya paliurus* today. This possibility is further supported by the presence of four small pointed structures often found on extant *Cyclocarya* fruits that occur in the position of stamens, or staminate. Although some authors have interpreted these structures as calyx lobes (e.g., Manning, 1938), this seems unlikely.

On the other hand, Manning (1938) noted that these same structures might be rudimentary stamens (or staminodes), an interpretation that does not appear to have been supported by other authors (Manos and Stone, 2001). Among many different dicot families with unisexual flowers there remain the rudimentary, nonfunctional structures of androecia or gynoecia (Mitchell and Diggle, 2005). For example stamens with fully formed pollen have been seen on fruits of *Liquidambar styraciflua* L. (Altingiaceae; K B Pigg, personal observation, 2004). It may be that the fossil *Cyclocarya* fruits are simply showing similar, rudimentary structures.

It is further intriguing that along with these unusual pollen-bearing structures on fruits, a pollen catkin with floral features strongly resembling those of extant *Cyclocarya* pollen catkins has been found in the Almont matrix (Fig.

15). We have not yet successfully recovered pollen from these catkins, however its presence suggests that if this catkin belongs to *Cyclocarya* (and no other juglandaceous megafossil is currently known from the site), then *brownii* may have produced both bisexual flowers and typical unisexual pollen catkins as well.

Fruit dispersal in Cyclocarya brownii—Both extant *Cyclocarya paliurus* and fossil *C. brownii* have been assumed to be wind-dispersed fruits (Stone, 1973; Manchester and Dilcher, 1982; Manos and Stone, 2001). This seems the obvious mode of dispersal since *Cyclocarya* has a large, distinctive circular wing, and winged diaspores (seeds and fruits) are well known to be wind dispersed (Burrows, 1975; Green, 1980; Green and Johnson, 1986; Augspurgur, 1986; Mirle and Burnham, 1999; Manchester and O’Leary, 2010). Numerous authors have recognized several patterns of motion among wind-dispersed diaspores that vary in relationship with the shape and attachment of the wing or wings (e.g., “helicopters”, “parachutes” and “gliders”, and “flutterers”, Burrows, 1975).

Highly asymmetrical fruits, such as “helicopters”, (e.g., samaras, *Acer*) have an unequal weight distribution and use the wing to create lift, counteracting acceleration due to gravity, resulting in a spin. A second type, “parachuters” or plumed fruits (e.g., dandelions, *Taraxacum*) have a centralized mass with apically attached wings. The wings create an umbrella effect because the movement of the air over the umbrella creates a suction in the direction of movement, resulting in an upward and forward lift, which slows its fall, while the back side generates a

90° drag to add to the forward motion. A third type, “flutterers”(e.g., soapberry, *Dodonea*) are bilaterally symmetric with two laterally attached wings with a deep apical and basal cleft. “Flutterers” have two possible patterns. One type is Phugoid oscillation, where the wings swap kinetic and potential energy back and forth between each other, resulting in a fluttering circular motion along a central gravitational vector from the release point. The second potential movement pattern for flutterers is a non-oscillatory mode where the fruit have a tumbling motion with no predictable path.

All of these examples are dependent on the asymmetry of the wing structure to maintain movement after an initial “push”. In contrast, in *Cyclocarya* the wing is symmetrically circular around the nutlet, a state that is uncommon in wind-dispersed fruits. The problem with having a symmetrically circular wing is that there is no torque or “spinning” motion produced upon dispersal. Consequently, there is little to no force counteracting gravity, as in asymmetric diaspores. *Cyclocarya* fruits lack the morphological features that would result in spinning, parachuting, or gliding. As to fluttering, even though the wings of *Cyclocarya* fruits are symmetrical they might tumble initially a short distance from the tree, but lack the asymmetrical morphologies of asymmetrical wings to account for Phugoid oscillation or spiral divergence.

A second critical attribute of *Cyclocarya* fruits is their highly sclerified structure. The effects of sclerified fruit wall and/or seed coats on germination are well documented in many plant species and include mechanical constraints,

prevention of water and oxygen uptake, and retention, or production of chemical inhibitors (Taiz and Zeiger, 2002). The germination time of *Cyclocarya* in nature is ~2 years (Fang et al., 2006). This is largely due to the dormancy caused by the thick, impermeable nutlet that surrounds the embryo. Experimental studies of *C. paliurus* fruits documented that germination times can be shortened by mechanical and chemical (with H₂SO₄) scarification and the treatment of gibberellic acid. Since chemical scarification and application of gibberellic acid is not a commonly occurring phenomenon in nature, the results due to mechanical scarification or abrasion are the only ones useful to infer what pre-germination events may occur to fossil *Cyclocarya*.

A third factor to consider in regards to fruit dispersal in *Cyclocarya* is the plant habitat. *Cyclocarya paliurus* grows in riparian zones today, in the montane regions of China mostly 420-2500 meters in elevation. In late summer, the fully mature fruits fall from the tree to be dispersed. Although dispersal has always been thought to be by wind, it may be at least equally likely that the fruits are water dispersed. Considering that mechanical scarification is critical for breaking dormancy and allowing for germination, it is likely that fruits fall into a stream and are scarified by abrasion along the streambed. Additionally Fang et al. (2006) note that breaking dormancy is further stimulated by soaking fruits of *Cyclocarya* in cold water (1-5°C), a temperature that would be consistent with that of cold mountain streams. It is further interesting that water-dispersed diaspores have been characterized by (Roth, 1977) as having a thick,

impermeable and sclerotic outer shell, along with internal air space. The idioblasts of *Cyclocarya* fruits might, in some circumstances operate as air channels, thus creating a fruit more adapted for water, rather than wind dispersal.

This scenario is consistent to what is known about the Almont fossil locality, which is interpreted as part of a fluvial/lacustrine system (Pigg and DeVore, 2010). Although another component of the Almont flora, *Ginkgo* leaves, are relatively common in Tertiary floras, seeds are rare (Pigg and DeVore, 2010). Modern *Ginkgo* trees do not become reproductively mature until they are around 30 years old (Royer et al., 2003), and the presence of numerous *Ginkgo* seeds in the Almont flora suggests that this was a mature forest site (Pigg and DeVore, 2010). Additionally, the scarcity of juglandaceous leaves and the lack of small, presumably immature fruits of *Cyclocarya* suggests that samples at both Almont and Beicegel Creek suggest that the *Cyclocarya* fruits of uniform size are deposited together as a result of sorting, and that water dispersal would be as likely an agent as wind.

In summary, *Cyclocarya brownii* fruits from the Almont and Beicegel Creek floras are clearly assignable to the genus *Cyclocarya* on the basis of fruit characters. However, these fossils are distinct from those of modern *C. paliurus* in several ways. First, the infructescences of the fossils have fruits with long pedicels demonstrating that they came from racemes, in contrast to modern *Cyclocarya* fruits which generally lack pedicels and which came from inflorescences that were spikes. The fossil infructescences have more fruits per

fruiting axis in comparison to the extant ones, and fruits of the fossil are smaller than those today. This combination of features may demonstrate a streamlining effect or reduction and change of the flower form in modern *Cyclocarya* as compared to the earlier fossil form.

Anatomically preserved specimens demonstrate that the wing of *Cyclocarya brownii* diverges from the equator of the nutlet just like the modern form, rather than expanding from the base of the fruit. This previous interpretation was based on looking at longitudinally fractured surface specimens (Manchester and Dilcher, 1982). The tissue that makes up the wing does, however, extend all the way around, cupping the base of the nutlet in both *C. brownii* and extant forms.

The sclerenchyma distribution in fruit walls documents greater complexity of the nutshell than previously described. Sclereids are not only isodiametric as previously assumed for the Juglandoideae, and idioblasts are present both in an outer layer and interdispersed throughout the fruit wall.

Fruits can have attached stamens with mature pollen. Whether this feature is typical of *Cyclocarya brownii* or only occasionally encountered is unclear at this point.

Lastly, *Cyclocarya* fruits have been assumed to be wind-dispersed because they have a large wing. However, the symmetrical wing is not aerodynamically suitable for significant dispersal (Burrow, 1975). Supporting evidence from studies of extant *Cyclocarya* germination suggests significant scarification of the

thick fruit wall is necessary to break dormancy, and that soaking in water further promotes germination (Fang et al., 2006). Plant habit of modern *Cyclocarya* is riparian. The lack of junglandaceous foliage or immature fruits, and the abundant, nearly uniform size of fruits suggests that some sorting occurred in both the Almont low energy and Beicegel Creek higher energy depositional environments. Dispersal by water is at least as likely as by wind.

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APPENDIX I
LIST OF MEASURED SPECIMENS

A list of the 101 specimens studied in detail for this project. The wing width is defined as the length from the edge of the nutlet to the margin of the wing at the widest point. The nut radius is defined as the length from the center of the nutlet to the edge where the wing is attached. Shape is determined using the margin of the wing. If a pedicel is present, it is measured from the base of the nutlet. The accession numbers are given for the specimens. Blanks indicate the data was missing or the fossil was not preserved in a way to discern the information.

Specimen	Wing Radius	Nut Radius	Shape	Pedicel	Acc. Number
1	16.0	5.0	round		B Cyclo B1
2	13.0	6.0	round	15	B Cyclo B2
3	12.0	5.0		18	B Cyclo B3
4	8.0	4.0	wavy		B Cyclo B4
5	11.0	4.0	oval		B Cyclo B5
6	10.0	4.0	round		B Cyclo B6
7	12.0	6.0	wavy	16	B Cyclo B7
8	10.0	5.0		14	B Cyclo B8
9	17.0	5.0	round	17	B Cyclo B9
10	14.0	6.0	wavy	21	B Cyclo B10
11	10.0	4.0	round	17	B Cyclo B11
12	13.0	6.0	wavy		B Cyclo B12
13	8.0	4.0	round		B Cyclo B13
14	9.0	4.0	round	13	B Cyclo B14
15	9.0	4.0	oval		B Cyclo B15
16	12.0	4.0			B Cyclo B16
17		4.0			B Cyclo B17
18	9.0	5.0	oval		B Cyclo B18
19	8.0	4.0	round		B Cyclo B19
20	12.0	5.0	oval	17	B Cyclo B20
21	10.0	5.0			B Cyclo B21
22	17.0	5.0	round		B Cyclo B22
23		5.0			B Cyclo B23
24	12.0	5.0			B Cyclo B24
25	12.0	6.0	wavy	15	B Cyclo B25
26	12.0	5.0	round		B Cyclo B26

27	9.0	4.0	wavy		B Cyclo B27
28	10.0	5.0			B Cyclo B28
29	13.0	5.0		19	B Cyclo B29
30		4.0		18	B Cyclo B30
31		4.0		25	B Cyclo B31
32	11.0	5.0			B Cyclo B32
33	13.0	5.0	wavy	17	B Cyclo B33
34	12.0	4.0	round		B Cyclo B34
35		5.0			B Cyclo B35
36	11.0	4.0	wavy	17	B Cyclo B36
37	14.0	5.0	round	19	B Cyclo B37
38		5.0			B Cyclo B38
39	11.0	4.0	round	10	B Cyclo B39
40	10.0	5.0	oval		B Cyclo B40
41	11.0	4.0	round		B Cyclo B41
42	10.0	5.0	round		B Cyclo B42
43		4.0			B Cyclo B43
44	13.0	6.0			B Cyclo B44
45	10.0	5.0	round		B Cyclo B45
46	14.0	5.0	wavy		B Cyclo B46
47		5.0	round		B Cyclo B47
48	7.0	4.0	round	8	B Cyclo B48
49	10.0	4.0		11	B Cyclo B49
50	9.0	5.0			B Cyclo B50
51	13.0	4.0	oval		B Cyclo B51
52	14.0	4.0	round	14	B Cyclo B52
53	13.0	5.0	wavy		B Cyclo B53
54	13.0	5.0	wavy	20	B Cyclo B54
55	14.0	5.0	wavy		B Cyclo B55
56	11.0	5.0		17	B Cyclo B56
57		5.0		25	B Cyclo B57
58	15.0	5.0	round		B Cyclo B58
59	8.0	4.0	oval		PP53650
60	10.0	4.0	wavy		PP53649
61	18.0	5.0	wavy	15	PP53654
62	15.0	5.0	wavy	16	PP53643
63	12.0	5.0			PP53642
64	11.0	4.0	oval	12	PP53653
65	12.0	5.0	wavy		PP53647
66	10.0	4.0	oval		PP53644
67	12.0	5.0			PP53648
68	13.0	5.0			PP53648

69	11.0	5.0			PP53644
70	13.0	4.0			PP53641
71	11.0	4.0	round	13	PP53645
72	10.0	4.0	oval		PP53651
73	10.0	4.0	round		PP53652
74	13.0	4.0	round		PP53640
75	10.0	4.0			PP53646
76	11.0	4.0	round	20	ASU Cyloc 6
77	9.0	4.0	round		ASU Cyloc 7
78		6.0			ASU Cyloc 8
79	10.0	4.0	oval		ASU Cyloc 9
80	10.0	4.0			ASU Cyloc 10
81	7.0	4.0	oval		ASU Cyloc 11
82	10.0	4.0			ASU Cyloc 12
83	11.0	4.0	oval		ASU Cyloc 13
84		5.0		17	ASU Cyloc 14
85	10.0	5.0		13	ASU Cyloc 15
86		5.0			ASU Cyloc 16
87		4.0			ASU Cyloc 17
88	10.0	5.0			ASU 10058
89	9.0	4.0			ASU 10029
90	12.0	4.0			ASU 10035
91	15.0	5.0			ASU 10074
92	11.0		wavy		ASU 10079
93	11.0	4.0	round		ASU 10112
94	12.0	5.0			ASU 10142
95	10.0	4.0	wavy		ASU 10122
96	10.0	4.0			ASU 10119
97	15.0	5.0	wavy	14	ASU 10117
98	8.0	3.0	wavy		ASU 10175
99	12.0	6.0	oval	15	ASU 10167
100	10.0	5.0	round		ASU 10194
101	8.0	4.0		11	ASU 10231

	Wing Width	Nut Height	Pedicel
Mean	11.3	4.6	16.03030303
Mode	10	4	17
Median	11.0	5.0	16
Max	18.0	6.0	25.0
Min	7.0	3.0	8.0

