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Floristic composition and variation in late Paleocene to early Eocene floras in North America

KATHLEEN B. PIGG & MELANIE L. DEVORE



The late Paleocene and early Eocene megafossil floras in North America are found primarily in the Williston, Green River, Powder River, Bighorn, and Alberta Basins of the northern Rocky Mountains and Western Interior. A few rare sites occur in the Mississippi Embayment of the Southeast. In contrast to the abrupt floristic changes seen at the K/T boundary, these floras document a gradual transition in species turnover, or, in the case of the Bighorn Basin, a long-term decrease in taxonomic diversity. This gradual transition is also in marked contrast to the rapid speciation among mammals of the early Eocene. Both preservation, and ability to place these floras within a temporal scale, determine how useful they are in assessing floristic changes across the Paleocene-Eocene transition. In some regions such as the Bighorn Basin of Wyoming precise stratigraphic control has allowed for documentation of paleoclimate change at a highly resolved temporal scale. At others, such as the Almont flora of the Williston Basin in North Dakota, exceptional preservation has provided the basis for describing individual taxa with the precision necessary to better understand their evolutionary and biogeographical histories. This study examines well-known plant taxa in the late Paleocene and early Eocene in the context of their depositional settings and temporal and spatial distribution. Integration of paleoecological and taxonomic studies is critical to understanding the evolutionary and depositional history of early Paleocene vegetation of North America. • Key words: Almont/Beicegel Creek flora, Bighorn Basin, Eocene thermal maximum, Fort Union Formation, Golden Valley flora, Joffre Bridge, Paleocene/Eocene Transition.

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In North America, late Paleocene to early Eocene megafossil floras are best documented for nonmarine strata of the Williston, Green River, Powder River, Bighorn, and Alberta (Western Canadian) Basins of the northern Rocky Mountains and Western Interior. In the Mississippi Embayment of the Southeast, confidently dated sedimentary sequences of these ages are rare. Interest in the Paleocene floras of North America has focused on floristic changes associated with the two major transitions, the K-T boundary at the beginning and the Paleocene to Eocene transition at the end. Whereas dramatic changes in floral diversity have been reported in connection with the K-T boundary (Wolfe & Upchurch 1987; K. Johnson 1992, 2002; Nichols & K. Johnson 2008), in the Paleocene to Eocene transition rates of extinction and origination were more gradual. This transition did not mirror the rapid Eocene radiation of modern mammals (Wing *et al.* 1995; Graham 1999). With rare exceptions, floras of the rest of the Paleocene have been regarded as relatively low diversity

assemblages (Wing 1998, K. Johnson & Ellis 2002). Nevertheless, they are essential for understanding the sources of major plant families that radiated later.

Early studies from the 1860's to early 20th century (*e.g.*, Newberry 1868; Lesquereux 1874, 1878; Ward 1885; Knowlton 1893, 1919) focused on identifying the living relatives of fossil plants and reconstructing Tertiary plant communities based on the ecological attributes of their extant descendants [Nearest Living Relative (NLR) techniques; Graham 1999]. From the mid-Century on, floristic studies documented many of the floras of western North America (see Graham 1999) and techniques for analyzing leaf morphological variation in relation to climate were developed [*e.g.*, Leaf Margin Analysis (LMA), Climate Leaf Analysis Multivariate Program (CLAMP)]. By the 1980s these techniques were used to score leaf types in fossil floras in order to estimate paleoclimate (Wolfe 1987). More recently, multiple proxies (carbon isotopes, pollen, leaf physiognomy) are placed in the context of radiometric and

biostratigraphic frameworks such as the North American Land Mammal Ages (NALMA, Wood *et al.* 1941, Woodburne 2004) to better correlate the responses of terrestrial ecosystems to the well-known marine systems. At the same time, detailed taxonomic studies of fossil plants have become increasingly valuable to the broader systematics community because they can be used to date nodes of divergence for clades within phylogenetic trees. In particular, well-preserved and complete specimens can serve as “key taxa” in phylogenetic reconstruction (Table 1).

As a consequence of the specialization of both of these areas, contemporary Tertiary paleobotanists have tended to focus on either paleoecology or systematics. Rarely have these various studies been integrated to present a comprehensive view of both the ecological response and evolutionary significance of Paleocene-Eocene plants. This paper reviews major studies of these two types and aims to help link these areas by (1) outlining the regional and depositional contexts of major late Paleocene and early Eocene megafossil floras in North America, (2) documenting “key taxa” that provide comprehensive taxonomic and phylogenetic information, and noting newly recognized taxonomic affinities; and (3) tracking the spatial and temporal distribution of selected genera that show major biogeographic patterns between the Paleocene and the Eocene.

Overview of the floras

Mississippian Embayment, Southeastern North America

Despite a rich plant megafossil record from the Eocene Wilcox and Claiborne Groups, sites representing the Paleocene-Eocene transition are extraordinarily rare in eastern North America (Graham 1999, Danehy *et al.* 2007). In general, floras from both the Atlantic Seaboard and the Gulf Coast occur in isolated clays and lignites that cannot be placed within the clear temporal framework required for tracing floristic changes across the Paleocene-Eocene transition. In the Southeast, the best documentation of the Paleocene-Eocene transition is based on pollen data that is currently being evaluated (Harrington 2003, 2004, 2008; Harrington & Jaramillo 2007).

The Paleocene-Eocene thermal maximum (PETM) probably has a position within the upper Tusahoma Formation in Mississippi as estimated by Harrington *et al.* (2005) based on palynomorph data from the Harrell Core. An early Eocene leaf flora from the Red Hot Truck Stop locality in Meridian, Mississippi is notable since it has been dated to the earliest Eocene and may fall within the PETM (Table 2). This site has a section exposing both the Tusahoma (Paleocene) and Bashi (Eocene) Formations

that have been placed into a chronological framework based locally on pollen, dinoflagellates, mammals and sequence stratigraphy as well as correlation with calcareous nannoplankton, and foraminifera (Danehy *et al.* 2007).

Fossil plants at the Red Hot Truck Stop occur within the basal Bashi Formation in a setting interpreted to represent a coastal environment that includes near-shore marine, tidal channels and estuary facies (Ingram 1991). The vegetation is considered to be tropical to subtropical and includes 18 leaf species and morphotypes. Notable elements are the climbing fern *Lygodium*, leaves of *Platycarya* (Juglandaceae), *Rhus* (Anacardiaceae), Fabaceae, Lauraceae, and Myrtaceae (Danehy *et al.* 2007). Leaves assigned to the malpighian family Ochnaceae represent some of the earliest megafossil records of the family (see also Pigg *et al.* 2005). Fruits of Icacinaceae and Juglandaceae are also known.

The Red Hot Truck Stop has significant potential to serve as a touchstone for reconstructing the Paleocene-Eocene floristic changes in the Mississippian Embayment. This locality also provides a rare megafossil datum for biogeographical relationships between eastern and western North American floras during the Paleocene-Eocene transition since several of the taxa described from the flora are also found in the West (*e.g.*, *Platycarya*, Ochnaceae, Myrtaceae, Danehy *et al.* 2007).

Western occurrences

In contrast to eastern North America, the Western Interior and Rocky Mountain regions provide a significant number of Paleocene and Eocene floras from sequences deposited within basins that can be placed within a chronological framework. Several of these sequences span the Paleocene-Eocene boundary. The easternmost of these is the central Williston Basin of North and South Dakota, Montana and the southern part of the Canadian provinces of Saskatchewan and Manitoba. In the southern region of the Williston Basin the Golden Valley flora localities span the Paleocene to Eocene boundary (Hickey 1977). To the north the Ravenscrag flora of Puercan-Torrejonian age has been described from Saskatchewan (McIver & Basinger 1993). The Bighorn, Green River, and Powder River Basins yield floras spanning the Paleocene-Eocene transition (Hickey 1980; Wing 1997, 1998; Wing *et al.* 1995, 2000; Gemmill & K. Johnson 1997; Wilf 2000). These last three basins have been the focus of numerous studies documenting floristic changes across the Paleocene-Eocene transition.

Other floras are of note because of the fidelity of preservation and details of taxonomic value. The Alberta Basin contains important floras at Genesee (Chandrasekaram 1974), Joffre Bridge and Munce's Hill near Red Deer, Alberta (Hoffman & Stockey 1999, Hoffman 2002). Detailed

Table 1. Key taxa. Late Paleocene and early Eocene taxa with detailed morphological and taxonomic information known. Locality abbreviations: in the Mississippian Embayment (ME): Red Hot Truck Stop (rhts); Bighorn Basin (BH); Green River Basin (GR); Powder River Basin (PR); Wind River Basin (WR); in the Williston Basin: Almont (al); Beicegel Creek (bc); Golden Valley (gv); Ravenscrag (rv); in the Alberta Basin (AB): Genesee (ge); Joffre Bridge (jb); Munce's Hill (mh); * indicates numerous floras. MT – Montana, WY – Wyoming.

Family	Taxon	Basin: Flora	Citation
Ricciaceae	<i>Ricciopsis speirsae</i>	AB: jb	Hoffman & Stockey (1997)
Ophioglossaceae	<i>Botrychium wightonii</i>	AB: ge	Rothwell & Stockey (1989)
Polypodiaceae	<i>Onoclea sensibilis</i>	AB: mh	Rothwell & Stockey (1991)
Blechnaceae	<i>Woodwardia</i> sp.	WB: bc, rv	McIver & Basinger (1993), Pigg <i>et al.</i> (2006)
Schizeaceae	<i>Lygodium kaulfussii</i>	ME: rhts; BH*	Manchester & Zavada (1987)
Thelypteridaceae	<i>Speirsopteris orbiculata</i>	AB: mh	Stockey <i>et al.</i> (2006)
Azollaceae	<i>Azolla stanleyi</i>	AB: jb	Hoffman & Stockey (1994)
Isoetaceae	<i>Isoetes horridus</i>	WB: bc, gv, rv	Brown 1962, Hickey (1977), McIver & Basinger (1993)
Cycadaceae	<i>Eostangeria pseudopteris</i>	GR*	Kvaček & Manchester (1999)
Cupressaceae	<i>Metasequoia foxii</i>	AB: mh	Falder <i>et al.</i> (1999, Stockey <i>et al.</i> (2001)
Betulaceae	<i>Cranea wyomingensis</i>	BH PR WR*	Manchester & Chen (1996)
Betulaceae	<i>Palaeocarpinus aspinosa</i>	BH, GR	Manchester & Chen (1998)
Betulaceae	<i>Palaeocarpinus dakotensis</i>	WB: al, bc	Manchester <i>et al.</i> (2005)
Betulaceae	<i>Palaeocarpinus joffrensis</i>	AB: mh	Sun & Stockey (1992)
Celtidaceae	<i>Celtis aspera</i>	BH	Manchester <i>et al.</i> (2002)
Cercidiphyllaceae	<i>Joffrea speirsae</i>	AB: jb	Stockey & Crane (1983); Crane & Stockey (1985, 1986a)
Cornaceae	<i>Cornus</i> sp.	WB: al, bc	Xiang <i>et al.</i> (2003)
Cornaceae	<i>Mastixia</i>	BH	Tiffney & Haggard (1996)
Hamamelidaceae	<i>Hamawilsonia boglei</i>	WB: al	Benedict <i>et al.</i> (2008)
Juglandaceae	<i>Cyclocarya brownii</i>	WB: al, bc	Manchester & Dilcher (1982)
Juglandaceae	<i>Polyptera manningii</i>	MT WY	Manchester & Dilcher (1997)
Lemnaceae	<i>Limnobiophyllum</i>	WB: rc; AB: jb	Stockey <i>et al.</i> (1997)
Myrtaceae	<i>Paleomyrtinea</i> sp.	WB: al, bc	Pigg <i>et al.</i> (1993)
Nymphaeaceae	<i>Nuphar wutuensis</i>	WB: al	Chen <i>et al.</i> (2004)
Nymphaeaceae	<i>Susiea newsalemae</i>	WB: al	Taylor <i>et al.</i> (2006)
Nyssaceae	<i>Amersinia, Beringiaphyllum</i>	WB: al, bc, gv	Manchester <i>et al.</i> (1999)
Nyssaceae	<i>Brownia</i>	WB: rv; WY	Manchester & Hickey (2007)
Nyssaceae	<i>Davidia antiqua</i>	WB: al	Manchester (2002a)
Polygalaceae	<i>Paleosecuridaca curtisii</i>	WB: al, bc	Pigg <i>et al.</i> (2008)
Sapindaceae	<i>Aesculus hickeyi</i>	WB: al, bc, gv	Manchester (2001)
Trochodendraceae	<i>Nordenskioldia, Zizyphoides</i>	WB: al, bc	Crane <i>et al.</i> (1991)

systematic studies from these Alberta sites include (1) at Genesee, *Botrychium*; (2) at Munce's Hill, the filicalean ferns *Onoclea*, *Metasequoia*, and *Palaeocarpinus*; and, (3) at Joffre Bridge, *Ricciopsis*, *Azolla*, *Joffrea*, Platanaceae and *Limnobiophyllum*.

In the Williston Basin, the Almont flora of central North Dakota (Crane *et al.* 1990) includes *Ginkgo*, taxodiaceous conifers, Taxaceae, *Cyclocarya* (Juglandaceae), Trochodendraceae, Myrtaceae, several cornalean taxa, *Aesculus*, *Acer*, *Palaeocarpinus* (Betulaceae), *Hamawilsonia* (Hamamelidaceae), *Paleoactaea* (Ranunculaceae),

Paleosecuridaca (Polygalaceae), and *Nuphar* and *Susiea* (Nymphaeaceae, Table 1, 3). This flora which has excellently preserved fruits and seeds, along with leaves is still under study (Manchester *et al.* 2004; Pigg & DeVore 2005, Pigg *et al.* 2008a, b; Benedict *et al.* 2007, 2008; Taylor 2006). Beicegel Creek is a second flora similar to Almont in taxonomic composition but with better anatomical preservation that allows for preparation with cellulose acetate peels and a more detailed stratigraphic context (DeVore *et al.* 2004; Pigg & DeVore 2003, 2005; Pigg *et al.* 2006, 2008a).

Table 2. Major floras discussed in text, excluding those of Bighorn Basin. Abbreviations: AL – Alberta; CO – Colorado; MS – Mississippi; MT – Montana; ND – North Dakota; SK – Saskatchewan; UT – Utah; WY – Wyoming; n – north; s – south; e – east; w – west; E – Early; M – Middle; L – Late. Data from ¹Danehy *et al.* 2007; ²Wilf 2000; ³Hickey 1977; ⁴McIver & Basinger 1993; ⁵Crane *et al.* 1990 and others (see Table 3); ⁶Manchester *et al.* 2004 and others (see Table 3); ⁷Stockey *et al.* 2006; ⁸Hoffman 2002; Hoffman & Stockey 1997; ⁹Chandrasekaram 1974.

Floras	Basin	Location No. sites	Age (Ma) NAML A	Formation (Member)	Depositional environments	MAT (°C)/ Vegetation	No. Species/ Morphotypes
¹ Red Hot Truck Stop	Mississippi Embayment	MS 1 site	55.8 earliest Wasatchian	Bashi (base)	tidal channels estuaries	tropical to subtropical	18 leaf & 2 fruit types
² Green River	Green River & subbasins	swWY 115 sites	Tiffanian-E Bridgerian	Fort Union- Wasatchian	alluvial, one lacustrine		
² Bison Basin	Great Divide	14 sites	56.2–60 Tiffanian	Fort Union	alluvial	11.7 humid warm temperate	29 species
² Clarkforkian & Big Multi	Green River	49 sites 15 sites	55.7 Clarkforkian	upper Fort Union lower Wasatch	alluvial	14.4, 18.6 humid subtropical	48 species 29 species
² Wasatch Main Body	Green River	6 sites	Graybullian to Lysitian	uppermost Fort Union	alluvial	dry mild	13 species
² Latham	Green River	7 sites	possibly Lysitian	Wasatch (Ranger Ranch)	alluvial	16.4 mild humid	17 species
² Sourdough	Green River	31 sites	52.8 probably E Lostcabinian	Wasatch (upper Ranger Ranch)	alluvial	21.3 humid	61 species
² Niland Tongue	Green River	5 sites	Lostcabinian	Wasatch	alluvial	23 warm	24 species
² Little Mountain	Green River	3 sites	E Bridgerian	Green River	lacustrine	19.6 hot arid	59 species
³ Golden Valley Bear Den	Williston	w ND sites	Clarkforkian	Golden Valley (Bear Den)	lowland forest swamp	warm temperate forest	41 species
³ Golden Valley Camels Butte	Williston	w ND sites	56 Wasatchian	Golden Valley (Camels Butte)	alluvial plain	subtropical	37 species
⁴ Ravenscrag	Williston	sw SK sites	Puercan–Torrejon ian	Ravenscrag	alluvial plain meandering streams ponds, swamps & lowland forest	polar broadleaf deciduous forest	46 species 23 unknown
⁵ Almont	Williston	c ND 1 site	57 Tiffanian 3	Sentinel Butte	clay lens channel fills altered by iron & silica solution	warm temperate forest	48 species 28 families
⁶ Beicegel Creek	Williston	w ND 5 sites	57 Tiffanian 3	Sentinel Butte	floodplain; fluvial & abandoned channel; swamp; cravasse splay	warm temperate forest	30 species
⁷ Munce’s Hill	Alberta	sc AL 1 site	57 Tiffanian T4	Paskapoo	wetland forest community	polar broadleaf deciduous forest	9 species
⁹ Joffre Bridge Roadcut	Alberta	sc AL 1 site	58-60 Tiffanian T3	Paskapoo	floodplain; fluvial & abandoned channel; swamp; cravasse splay	polar broadleaf deciduous forest	28 genera 18 families
⁹ Genessee	Alberta	sc AL 1 site	Tiffanian	Paskapoo	wetland forest community	polar broadleaf deciduous forest	19 species

Stratigraphic and depositional settings in Western North America

Numerous studies of the Paleocene-Eocene transition in continental strata in North America have focused on sequences present in the Bighorn and Williston Basins (Table 2, 4, 5). A brief explanation of the origin of the basins in the Rocky Mountains, as well as the region of the Williston Basin to the east of the Rockies, is useful for understanding the Paleocene-Eocene depositional environments and stratigraphy.

During the Cretaceous, a large foreland sedimentary basin spanned from the Arctic Ocean to the Gulf of Mexico. At the end of the Cretaceous and through the Eocene, crustal shortening and deformation associated with the

Laramide orogeny dissected the foreland basin into a series of smaller basins that became well established by the end of the Paleocene (Fig. 1; Hamilton 1988, Flores *et al.* 1994, Perry *et al.* 1991, R. Johnson & Flores 1998). East of the Rocky Mountains, arches associated with Laramide deformation, including the Black Hills and Bighorn Mountains, influenced the geometry of both the Powder River and Williston Basins. Mid-continental arches, sometimes referred to as “plainstyle folding”, developed in the region now occupied by Kansas, Minnesota, Nebraska, North Dakota, Oklahoma and Texas. The origin of mid-continental arches is estimated to be at least Late Paleozoic, even older, and they were probably activated during the Laramide orogeny (Bunker *et al.* 1988, Tikoff & Mason 2001).

Bighorn Basin

The Bighorn Basin is located adjacent to the Pryor Bighorn Mountain Block to the east with the downdropped Red Lodge Block and uplifted Beartooth Block oriented perpendicular to its western border. The Columbus “Shelf” separates the Bighorn Basin from the Crazy Mountains Basin towards the northwest. These structural areas were elevated during the mid-late portion of the Laramide orogeny, with the uplift of the Beartooth Mountains occurring during the middle to late Paleocene (Beck *et al.* 1988), while that of the Bighorn Mountains is dated at late Paleocene. During the early Eocene the southern Bighorn Mountains were thrust towards the southeast. Clearly, the tectonic history had an influence on depositional environments located within the basin, impacting the types and directions of fluvial systems present.

Thick sequences of clastics (sandstones, mudstones), lignites, and freshwater carbonates were deposited during the Paleocene and early Eocene (Gingerich 1983). The thick (3000 m), Paleocene sequences of clastics and lignites present in the Bighorn Basin are assigned to the Fort Union Formation. The gray-light brown beds of the Fort Union Formation are overlain by the oxidized mudstone dominated Willwood Formation (Paleocene to early Eocene, T. Brown & Kraus 1981). Based on geometry, Wing (1984), recognized two distinct sedimentary units within the Willwood Formation, lenticular bodies and tabular bodies, and characterized the plant fossil assemblages within each. The lenticular bodies, were interpreted as reflecting deposition within abandoned fluvial channels while the tabular bodies, composed of underbeds, carbonaceous shales, interlaminated silts and shales, and overlying sand bodies, were thought to be the remains of backswamp deposits on a distal floodplain (Wing 1984). Further study of the backswamp deposits (Davies-Vollum & Wing 1998) demonstrated that they are prevalent in the lower and upper Willwood Formation, but are conspicuously absent in the middle portion. An explanation for this lack of backswamp deposits in the middle Willwood Formation is that enhanced rates of sediment accumulation resulted in organic material becoming dispersed within the sediments and then being degraded in a drier climatic regime before preservation could occur. A combination of climatic and tectonic influences was responsible.

A comprehensive magnetostratigraphic framework has been developed recently for the Bighorn Basin (Clyde *et al.* 2007), making it possible to compare interpretations of faunal and floral turnovers and correlate other paleoclimatic data with worldwide databases. One of the outcomes of this study was the documentation of the time-transgressive elements of basin formation and demonstration that the northern and southern parts of the basin had dis-

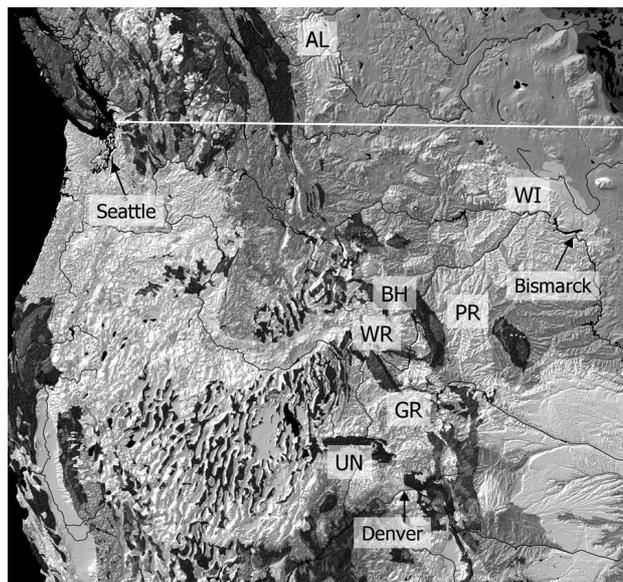


Figure 1. General overview of major Paleocene-Eocene basins in the Rocky Mountains and Great Plains of western North America. Abbreviations: AL – Alberta, BH – Bighorn, GR – Green River, PR – Powder River, UN – Uinta, WI – Williston, WR – Wind River. The cities of Denver, Colorado; Seattle, Washington, and Bismarck, North Dakota are indicated for context. Redrawn from Barton *et al.* (2009).

tinct depositional histories, thus permitting interpretation of regional elements influencing the plant fossil record. Key taxa from the Bighorn Basin include the following: *Palaeocarpinus aspinosa* and *Cranea* (Betulaceae), *Polyptera* (Juglandaceae), *Mastixia* (Cornaceae), and *Celtis aspera* (Celtidaceae, Table 1).

Green River Basin

The Green River Basin occupies southwestern Wyoming and portions of Colorado and Utah and includes both the Green River Basin proper and a series of subbasins including the Great Divide, Sand Wash, Vermilion Creek and Washakie Basins, (as well as a locality, the Bison Basin; Wilf 2000). To the south, the Green River Basin is separated from the Uinta Basin by the Uinta Mountains, and in the north from the Wind River Basin by the Wind River Mountains (Fig. 1). The western border of the Green River Basin is bounded by a complex series of imbricated thrust faults comprising the Sevier Belt. The easternmost of these thrust belts, the Hogsback Thrust, is the youngest and forms the boundary of both the Green River and Uinta Basins (DeCelles 1994). The Rock Springs Uplift segmented the Green River Basin proper from the Sand Wash Basin to the south, and the Washakie and Great Divide Basins to the north (Roehler 1993). Assemblages of sedimentary rocks spanning the late Cretaceous through the middle Eocene are found within the Green River Basin. The Paleocene is represented by fluvial

Table 3. Almont and Beicegel Creek floras, Megafossil Occurrences. ** – detailed published description; * – short published description/photos; ^{AB} – abstract; ^{PC} – personal communication. Name is not always the same in Crane *et al.* (1990), but figure number indicates specimen.

Family	Genus	Plant part	Almont	Beicegel Creek	References
PTERIDOPHYTES					
Blechnaceae	<i>Woodwardia</i> sp.	fronds	–	rare	*Pigg <i>et al.</i> (2006), figs 4, 7
Ferns	Filicalean fern	frond, spores	–	rare	^{AB} Matthews <i>et al.</i> (2006)
Isoetaceae	<i>Isoetes</i> cf. <i>horridus</i>	megaspores	–	rare	^{AB} Matthews <i>et al.</i> (2007)
GYMNOSPERMS					
Ginkgoaceae	<i>Ginkgo adiantoides</i>	leaves, seeds, ovulate stalks	abundant	common	*Crane <i>et al.</i> (1990), fig. 2
Cupressaceae	cf. <i>Parataxodium</i> sp.	leaves seeds pollen and seed cones seeds	abundant	abundant	*Crane <i>et al.</i> (1990), figs 3, 4
Cupressaceae	<i>Metasequoia</i>	seeds	rare	–	^{PC} Manchester
Pinaceae	cf. <i>Pinus</i>	ovule cone	–	rare	^{PC} Manchester
Taxaceae	<i>Diploporus</i>	seeds	occasional	occasional	*Crane <i>et al.</i> (1990), fig. 25J
Taxaceae	<i>Torreya</i>	seeds	rare	–	^{PC} Manchester
ANGIOSPERMS					
Actinidiaceae	cf. <i>Saurauia</i>	seeds and fruits	occasional	common (seeds)	*Crane <i>et al.</i> (1990), fig. 24A–E ^{AB} Pigg & DeVore (2003)
Araliaceae	<i>Toricellia</i>	fruit	rare	–	*Manchester <i>et al.</i> (2009)
Betulaceae	<i>Palaeocarpinus dakotensis</i>	infructescence fruits seeds pollen catkins pollen	abundant	abundant	*Crane <i>et al.</i> (1990), fig. 16, 17 **Manchester <i>et al.</i> (2004)
Betulaceae	<i>Corylites</i> sp.	leaves	abundant	abundant	*Crane <i>et al.</i> (1990), fig. 18A, B **Manchester <i>et al.</i> (2004)
Cercidiphyllaceae	<i>Nyssidium arcticum</i>	fruits, seeds, leaves	occasional	–	*Crane <i>et al.</i> (1990), fig. 10
Cornales	<i>Amerisinia obrullata</i>	fruits, seeds	common	abundant	*Crane <i>et al.</i> (1990), fig. 24F–H **Manchester <i>et al.</i> (1999)
Cornales	<i>Beringiaphyllum</i>	leaves	abundant	common	*Crane <i>et al.</i> (1990), fig. 30 **Manchester <i>et al.</i> (1999)
Cornales	cf. <i>Cornus</i> sp.	endocarps	rare	occasional	*Crane <i>et al.</i> (1990), fig. 20G–I *Xiang <i>et al.</i> (2003), fig. 3H
Cornales	<i>Davidia antiqua</i>	infructescence fruit, leaves	common	–	*Crane <i>et al.</i> (1990) **Manchester (2002a)
Cornales	cf. <i>Diplopanax</i>	endocarp	occasional	–	^{PC} Manchester
Hamamelidaceae	<i>Hamawilsonia bogle</i>	infructescence with seeds	occasional	–	*Crane <i>et al.</i> (1990), fig. 15 **Benedict <i>et al.</i> (2008)
Hamamelidaceae	seeds	seeds	rare	–	*Crane <i>et al.</i> (1990), fig. 27E–G **Benedict <i>et al.</i> (2008)
Hamamelidaceae	pollen catkins with <i>in situ</i> pollen	pollen catkins, pollen	rare	–	*Crane <i>et al.</i> (1990) **Benedict <i>et al.</i> (2008)
Icacinaceae	<i>Icacinicarya collinsonae</i>	endocarp	1 specimen	–	**Pigg <i>et al.</i> (2008b)
Icacinaceae	<i>Icacinicarya dictyota</i>	endocarp	–	1 specimen	**Pigg <i>et al.</i> (2008b)
Icacinaceae	<i>Palaeophytocrene</i>	endocarps	rare	rare	*Crane <i>et al.</i> (1990), fig. 22A–C
Juglandaceae	<i>Cyclocarya brownii</i>	fruits, infructescence	common	common	**Manchester & Dilcher (1982) *Crane <i>et al.</i> (1990), fig. 8C, D, F, G ^{AB} Taylor (2007)
Juglandaceae		leaves	rare	–	*Crane <i>et al.</i> (1990), fig. 19
Meliosmaceae	<i>Meliosma rostellata</i>	fruits	common	common	*Crane <i>et al.</i> (1990), fig. 21
Menispermaceae	cf. <i>Canticocculus</i>	fruits	rare	–	*Crane <i>et al.</i> (1990), fig. 5
Menispermaceae	cf. <i>Tinomiscium</i>	fruit	rare	–	^{PC} Manchester
Myrtaceae	<i>Paleomyrtinea</i>	fruits and seeds	occasional	common	*Crane <i>et al.</i> (1990), fig. 20A–E **Pigg <i>et al.</i> (1993), figs 18–22, 24

Table 3. continued

Family	Genus	Plant part	Almont	Beicegel Creek	References
Nymphaeaceae	<i>Susiea newsalemae</i>	seeds	rare	rare	** Taylor <i>et al.</i> (2006)
Nymphaeaceae	<i>Nuphar wutuensis</i>	seeds	1 specimen	1 specimen	** Chen <i>et al.</i> (2005)
Ochnaceae	<i>Ochna</i> sp.		rare	rare	* Crane <i>et al.</i> (1990), fig. 26A–C AB Pigg <i>et al.</i> (2005)
Platanaceae	<i>Macginicarpa</i>	infructescence	rare	–	PC Manchester
Platanaceae	unnamed	pollen catkin	rare	–	* Crane <i>et al.</i> (1990)
Platanaceae	<i>Macginitiea</i>	leaves	occasional	occasional	PC Manchester
Platanaceae	leaf types a, b, c	leaf	rare	–	* Crane <i>et al.</i> (1990), fig. 11
Polygalaceae	<i>Paleosecuridaca curtisii</i>	fruit	common	rare	* Crane <i>et al.</i> (1990), fig. 23A–C ** Pigg <i>et al.</i> (2008a)
Ranunculaceae	<i>Paleoactaea nageli</i>	fruit and seeds	rare	rare	* Crane <i>et al.</i> (1990), fig. 25D–F ** Pigg & DeVore (2005)
Sapindaceae	cf. <i>Acer</i>	fruit	common	common	* Crane <i>et al.</i> (1990), fig. 22B–D AB Kittle <i>et al.</i> (2005)
Sapindaceae	<i>Aesculus</i>	leaf	rare	–	** Manchester (2000)
Sapindaceae	cf. <i>Sapindus</i>	fruit	rare	–	PC Manchester
Trochodendraceae	<i>Nordenskioldia borealis</i>	fruit	common	common	* Crane <i>et al.</i> (1990) ** Crane <i>et al.</i> (1991)
Trochodendraceae	<i>Zizyphoides flabella</i>	leaf	abundant	common	* Crane <i>et al.</i> (1990) ** Crane <i>et al.</i> (1991)
Vitaceae	<i>Ampelocissus</i>	leaf	rare	rare	PC Manchester
Zingiberales	<i>Spirematospermum</i>	embryo, seed	occasional	abundant	* Crane <i>et al.</i> (1990), fig. 26D–F AB Benedict <i>et al.</i> (2007)
Incertae sedis	<i>Averrhoites affinis</i>	leaf	occasional	occasional	* Crane <i>et al.</i> (1990), fig. 31
Incertae sedis	<i>Porosia verrucosa</i>	seed	occasional	occasional	* Crane <i>et al.</i> (1990), fig. 29C, D ** Manchester (2002b)
Incertae sedis	monocot	leaves, rhizomes	rare	abundant	* Crane <i>et al.</i> (1990), fig. 29a, b AB DeVore <i>et al.</i> (2004)
Incertae sedis	fruits, seeds, leaves	fruits, seeds, leaves			* Crane <i>et al.</i> (1990)

deposits assignable to the Fort Union Formation while the Wasatch Formation, also reflecting a fluvial deposition, extends from the early to middle Eocene and interfingers with the lacustrine, early and middle Eocene Green River Formation (Roehler 1985, 1993; Wilf 2000).

To assess climate changes across the Paleocene-Eocene boundary, Wilf (2000) sampled seven floral assemblages spanning the boundary. The first and lowermost assemblage is from the Bison Basin locality in the Fort Union Formation in the Great Divide Basin, and is of Tiffanian age (Gemmill & K. Johnson 1997). The second assemblages (2 and 2a of Wilf 2000) are the Clarkforkian and Big Multi Quarry floras, of early Clarkforkian age, which span the upper Paleocene Fort Union Formation in southern Wyoming and provide its youngest records. The third assemblage, from the Wasatch Main Body, generally has a sandy lithology with numerous oxidized beds and occasional weathered, carbonaceous deposits. Plant material is both infrequent and low in diversity. Further

upsection, the fourth assemblage is a tabular carbonaceous shale unit from the Ramsey Ranch Member of the Wasatch Formation above the Latham 4 coal, which yields slightly better preserved material. The fifth is the Sourdough assemblage, which comprises a set of sites, located just upsection from the Latham 4 coal in the uppermost Ramsey Ranch Member of the Wasatch Formation and associated with the Sourdough 2 coal zone. Floristically, the Sourdough assemblage is very similar to the Elk Creek section in the Bighorn Basin (Davies-Vollum & Wing 1998) and provides some interbasinal comparison between the Bighorn and Green River Basins. The sixth assemblage is the Niland Tongue from the last fluvial unit sampled in the early Eocene, and the seventh and last assemblage is the Little Mountain assemblage of early Bridgerian age from the lacustrine Green River Formation.

Wilf's (2000) detailed treatment of these data using leaf-margin and leaf area analyses, as well as assessment of the climatic tolerances of nearest living relatives for

paleoclimate analysis, provided a rich record of climate change between the Paleocene and Eocene in the Green River Basin. In conjunction with analyses of leaf floras, Wilf estimated numbers of “species” based on counts of both formally described species and leaf morphotypes to track changes in floral diversity. Two floral turnovers, the first representing the Clarkforkian-Wasatchian warming and the second associated with the Wasatchian-Bridgerian drying interval, are documented (Table 2). More than 80% of the “species” were affected by these two events.

The studies described above represent an important initial step in understanding the interrelationships between regional and global signals. Because people want to use these results to correlate global climate events, it is important to tease out the local and regional influences. Clearly, integrative studies interweaving details of the tectonic events influencing the development of these basins, as well as patterns of paleodrainage and depositional systems, enhance the ability to unravel local, regional and global signals present in the multitude of proxy data sets based on paleontological sources.

Williston Basin

The largest, easternmost of the basins associated with stratigraphic sequences spanning the Paleocene-Eocene boundary is the Williston Basin which covers parts of North Dakota, South Dakota, Montana in the USA and southern portions of the Canadian provinces of Manitoba and Saskatchewan (Fig. 1).

Today the Williston Basin is actually two basins. The Williston Basin proper is found to the NW with a second arm of the complex called the Powder River Basin. The two basins appear to meet at the Miles City Arch with the Williston Basin extending to the Black Hills and the Powder River Basin being roughly flanked on its east and west margins by the Black Hills and Bighorn Mountains. The present paper will focus on the depositional environments of the following floras of the Williston Basin: Ravenscrag, Almont, Beicegel Creek, Wannagan Creek, and Golden Valley.

The Williston Basin has a long history and numerous processes have influenced its formation, and there have been several interpretations regarding its development. One hypothesis is that the basin formed as a tensional response to shearing between two lineaments during the Paleozoic (Gerthard *et al.* 1982). The folding and faulting within the Williston Basin has been attributed to both movement along basement blocks and as a response to subsidence. Compared with other basins in the Great Plains and Rockies, the degree of faulting is slight and seismic surveys are necessary to document the nature and extent of

these faults. In particular, the faults associated with the Cedar Creek, Nesson, and Heart River Anticlines, have extremely steep dips and have experienced episodes of near vertical displacement. Some synclinal formations within the basin are attributed to collapse after the dissolution of Devonian age salt deposits.

The Williston Basin may appear to have a simple, layered stratigraphy, but the interplay of the tectonics and shifts in paleodrainage, clearly paint a more complex picture as illustrated by a recent study (Belt *et al.* 2004) on the unconformities and age relationships of the Tongue River and older members of the Fort Union Formation. Similar studies on the Sentinel Butte Member have not been undertaken.

Ravenscrag flora. – Another region, flanking the northern rim of the Williston Basin, has yielded fossil plant assemblages. The Paleocene Ravenscrag Formation of southwestern Saskatchewan does not extend stratigraphically across the Paleocene-Eocene boundary as is the case with the Golden Valley Formation from the Williston Basin of North Dakota (see below). However, the Ravenscrag Formation can be correlated with the Cretaceous (Maastrichtian) Hell Creek Formation up through most of the Bullion Creek Formation of North Dakota and is interpreted as Puercan to Torrejonian in age (McIver & Basinger 1993).

At the end of the Cretaceous, cratonic subsidence, in concert with subsidence caused by salt dissolution of the Devonian Prairie Evaporate (Broughton 1979, Frank & Bend 2004), caused deposition of thin (0.5–1.0 m) coal deposits with thicker beds (avg. 3.2 m) being deposited when cratonic and salt dissolution subsidence decreased during the Paleocene. Regional and local subsidence influenced sedimentation and makes correlation within and between the regional units difficult (Frank & Bend 2004).

The Ravenscrag Formation consists of lignite-bearing clay, silt and sand beds overlying the latest Cretaceous (Maastrichtian) Frenchman Formation. The beds assigned to the Ravenscrag Formation were deposited as an eastward-thickening wedge representing a low-energy fluvial-alluvial plain depositional system [S.G.S. (Saskatchewan Geological Survey) 1994, Frank & Bend 2004]. The site is interpreted as an alluvial plain with meandering streams, ponds, swamps and lowland forests.

The Ravenscrag flora represents a polar broadleaf temperate forest. Floral elements include woody dicots of Cercidiphyllaceae, *Cornophyllum* and a compound leaf type Platanaceae (*Platanites canadensis*) similar to those found at Mull, Scotland (Crane *et al.* 1988; Kvaček *et al.* 2001). Several filicalean ferns, including *Woodwardia gravis*, are present, and the common conifers include the cupressaceous genera *Mesocyparis* and *Glyptostrobus* while *Fokienia* and *Elatocladus* are present but uncommon. The most common type of fossil at this locality is the

dicot leaves that were assigned to *Dicotylophyllum anomalum* by McIver & Basinger (1993). The leaves are now considered assignable to *Browniea* (Nyssaceae; see Manchester & Hickey 2007). Interestingly, some elements that are often characteristic of Paleocene floras (e.g., *Ginkgo*, *Glyptostrobus*) are relatively rare here (McIver & Basinger 1993) or even lacking (Betulaceae). There is a diversity of aquatic forms, which include *Isoetes horridus*, two species of *Azolla*, the *Trapa*-like genus *Trapago*, the *Nelumbo*-like *Nelumbago*, and several rosette-forming monocots described as *Pistia* and *Spirodela* (now *Limnobiophyllum*, Stockey *et al.* 1997).

Studies of the Souris Lignite from the Ravenscrag (Frank & Bend 2004) indicate that transitional fern-dominated and *Taxodium*-dominated stable environments coexisted and suggest the Okefenokee Swamp (Georgia, USA) as a possible modern analogue. The Okefenokee also has been proposed as a modern analogue to the Tertiary peat-forming environments of the northern Great Plains (Rich 1979).

Wannagan Creek. – The Wannagan Creek site is well known for its rich assemblage of vertebrate faunas (predominately champsosaurs, crocodylians, turtles) but also contains beds bearing less studied plant material (Erickson 1991). The portion of the Bullion Creek Formation section at Wannagan Creek that has been the focal point for paleontological investigation lies 19.8 m above the contact with the underlying Sentinel Butte Formation (Melchior & Hall 1983).

Jacob (1972) and particularly Melchior & Hall (1983) have interpreted the depositional environment as representing a floodplain based on three distinct beds. The first is primarily fluvial and fines upwards from a coarse silt to a silty clay and contains remains of an aquatic plant community consisting of fossils identified as *Cabomba*, *Equisetum*, *Nelumbium*, *Sparganium*, and in situ corms assignable to *Isoetes horridus*. The second bed, a lignitic black shale rich in organics, is interpreted as an isolated channel segment and contains large branches and tree trunks, but identifiable plant megafossils are rare until the last, upper 5 cm of the bed, where leaves become abundant. It is in bed 2 that the articulated fossils of vertebrates are found. The third bed is a massive unit consisting of coarse silt and fining upward to clays. This third bed is interpreted as a flood surge or crevasse splay from an adjacent channel (Melchior & Hall 1983). Although several studies have focused on the palynomorphs, particularly the megaspores (e.g., Melchior & Hall 1983), the megafloora is not comprehensively illustrated and identifications of megafossil elements need to be verified.

Almont and Beicegel Creek floras. – The Almont flora was first described by Crane *et al.* (1990) and is unusual since

the plants are preserved both morphologically and anatomically (Table 3). The original site, located near the center of North Dakota, outcrops at the very surface and is impossible to place within a stratigraphic context. Based on the floral assemblage, the site was assigned to the late Paleocene Sentinel Butte Formation. The plant material is preserved in siliceous shale units that appear to represent clay lenses deposited in abandoned channels and then enriched by silica and iron-rich solutions. Whether the Almont site represents a single channel, or a set of small interfingered channels, is uncertain. However, it does appear that the fossil-bearing sedimentary units are discontinuous at the Almont site.

In 1999, a new site was found in the Beicegel Creek area of McKenzie County, in western North Dakota, with the siliceous shales found in place within a friable, gray sandstone (Table 3). Material collected from the Beicegel Creek region can be studied both by sectioning and SEM, (as can the Almont material), as well as by the cellulose acetate peel method (Joy *et al.* 1956, Basinger & Rothwell 1977). The amount of carbon preservation is exquisite in comparison to other silicrete beds found in the Sentinel Butte and Golden Valley Formations. This flora is much more diverse than the similarly preserved permineralizations described by Ting (1972) from younger strata associated with the Golden Valley flora. The geochemical circumstance permitting this preservation, combined with the high number of taxa shared by both the Almont and Beicegel Creek floras, in no way can be explained as being part of a single, widespread bed, but rather, represents deposition within the same meandering fluvial system (DeVore, personal observation).

The Sentinel Butte Formation has been characterized by the dominance of illite and montmorillonite clays, its olive-green color, orange-stained zones with nodules of siderite, “bentonite” layers, and the abundance of petrified conifer wood (Hickey 1977). Fischer (1953) observed petrified stumps below the Sentinel Butte-Golden Valley contact and Hickey (1977) noted a zone of stumps below the contact in areas including the Crooked Creek escarpment in southwestern Dunn County and eastern Stark County. During fieldwork in McKenzie County, the present authors have noted a zone of taxodiaceous conifer stumps present in some areas of the contact, but there also appears to be other zones of stumps present below the contact. Along with the lignite and petrified stump zones are plant-bearing beds that appear to be associated with channel fills (DeVore, personal observ.).

Golden Valley flora. – In North Dakota, the Sentinel Butte Formation is, in general, regionally conformably overlain by the Golden Valley Formation. In western North Dakota, these formations outcrop discontinuously on isolated but-

tes and are best exposed in the Little Badlands. Generally, the sequences of the Golden Valley Formation consist of paulstrine to fluvio-deltaic sequences and are divided into two members. The lower Bear Den Member is dominated by kaolinitic claystones and siltstones. The upper Camels Butte Member, in contrast, contains lenses of micaceous, crossbedded sandstones separated by finer-grained beds (Hickey 1977). Both members represent fluvial deposits, and occasionally, both the Bear Den and Camels Butte Members downcut into the underlying Sentinel Butte Formation. The current placement of the Paleocene-Eocene boundary is within the Bear Den (Clechenko *et al.* 2007). Hickey (1977) found 41 Golden Valley Formation localities containing fossil plant beds. Twenty-seven of these in the Bear Den Member were found in the lower 9.1 meters of the unit and would therefore, represent the latest Paleocene flora in the Williston Basin.

Carbon isotope values of bulk organic matter and palynostratigraphy were studied within the Golden Valley Formation to try to identify the PETM (Harrington *et al.* 2005, Clechenko *et al.* 2007). The “orange zone” identified within the Bear Den Member was interpreted as representing an episode of intense pedogenesis at *ca* 55 Ma based on the high abundances of iron-stained kaolinite, poor organic carbon preservation and the presence of features roughly equivalent to those found in modern laterites.

The Golden Valley flora was described from a series of approximately 70 localities in 6 transects across North Dakota (Hickey 1977). Of 82 total taxa, 52 are present at Bear Den and 42 at Camels Butte. Sixteen taxa are shared, including, most notably: *Equisetum*, *Glyptostrobus*, *Metasequoia*, *Porosia*, *Davidia* (listed as “*Viburnum antiquum*”, Manchester 2002a), *Cercidiphyllum*, *Cornus*, *Aesculus* (listed as *Carya antiqua*; see Manchester 2001), *Averhoites*, *Meliosma*, *Chaetoptelea*, and “*Ampelopsis*”, with 36 taxa unique to Bear Den and 24 to Camels Butte (Hickey 1977). Notable genera at Bear Den but not Camels Butte, include: the filicalean ferns *Osmunda* and *Woodwardia*, *Pinus prergrimus*, *Acer*, *Beringiaphyllum* (listed as *Viburnum cupanoides*, see Manchester *et al.* 1999), *Zizyphoides* (listed as *Cocculus flabella*, Crane *et al.* 1991). Camels Butte hosts *Isoetes horridus*, the small aquatic lycopod, and the aquatic floating heterosporous water fern *Salvinia*, leaves assigned to *Betula hesterena* (probably closely related to *Corylites* leaves of *Palaeocarpinus*). The Golden Valley flora apparently lacks *Ginkgo*.

Alberta Basin

Genesee, Munce’s Hill, and Joffre Bridge floras. – Paleocene aged floras have also been recovered from the Paskapoo Formation of south-central Alberta. The Paskapoo

Formation represents deposition by rivers that flow eastward from the cordillera to the Alberta Basin (Fig. 1). The basin parallels the cordillera and extends eastward into south-central Alberta for more than 600 km (Demchuk *et al.* 1991, Hoffman & Stockey 1999). The Paskapoo Formation can be correlated with the upper part of the Ravenscrag Formation (Demchuk *et al.* 1991).

The Paskapoo Formation yields three main productive sites at Genesee, Munce’s Hill and the Joffre Bridge Roadcut locality (Hoffman 2002). Of these, Genesee is the earliest studied site, and of relatively low diversity (19 taxa), with several significant elements typical of a polar deciduous flora (Chandrasekharam 1974). The flora is dominated by *Metasequoia* (36%) and *Cercidiphyllaceae* (around 33%), with additional representatives of *Glyptostrobus*, *Fokienia*, *Taxodium*, *Azolla*, *Platanus*, *Nordenskioldia*, a moss, and several ferns. This site boasts the only known fossil record of the ophioglossalean fern *Botrychium*, which has been reconstructed as a “whole plant” that bears a remarkable resemblance to its extant relative (Rothwell & Stockey 1989). Two typical taxa of the late Paleocene, *Betulaceae* and *Ginkgo*, apparently are lacking.

The Munce’s Hill locality contains a relatively low diversity assemblage (9 taxa) that has been interpreted as a wetland forest community (Stockey *et al.* 2006). This flora is dominated by *Metasequoia* and the fern *Onoclea*. *Metasequoia foxii* plants, including their seedlings, are known from both Munce’s Hill, and a second nearby and contemporaneous locality at Guo Mine. From these sites *Metasequoia foxii* has been reassembled as a “whole plant” (Falder *et al.* 1999, Stockey *et al.* 2001). Although taxodiaceous conifers are very common components of Paleogene floras, it is rare to find all of the separate organs together in the same horizon and in attachment to one another. *Metasequoia foxii* can be compared with *Metasequoia milleri*, another whole *Metasequoia* plant that is known from the Eocene Princeton Chert (Basinger 1981, 1984; Rothwell & Basinger 1979).

Another whole plant reconstruction from Munce’s Hill is that of the fern *Onoclea* (Rothwell & Stockey 1991). The authors placed this fossil fern into the modern species *O. sensibilis* because it is essentially identical in sporophyte and spore morphology to the extant plants. Rhizomes in growth position, bearing attached vegetative and fertile fronds, were uncovered carefully in the field and photographed in situ to demonstrate their morphology and plant habit. This was necessary because the beds have been severely affected by post-depositional cleavage perpendicular to the bedding plane, such that larger slabs bearing more complete fronds could not be recovered. Other taxa from Munce’s Hill include the thelypterid fern *Speirsiopteris orbiculata* (Stockey *et al.* 2006); *Palaeocarpinus joffrensis* (Sun & Stockey 1992);

Equisetum sp. (Vavrek 2002); a possible bryophyte; stem remains of *Joffrea*, and *Aphananthe*, of possible ulmaceous affinities; and the foliage type *Wardiaphyllum* (Stockey *et al.* 2006).

Hoffman & Stockey (1999) studied the depositional environment of the Joffre Bridge Roadcut locality, and recognized five depositional units: 1) floodplain; 2) fluvial channel; 3) abandoned channel; 4) swamp, and 5) crevasse splay. The floodplain deposits, which are capped by a paleosol with vertebrate remains, lack identifiable plant remains. Fluvial and abandoned channel sediments overlay the paleosol and contain remains of riparian trees (*e.g.*, Platanaceae, *Joffrea*). The fourth depositional unit, a carbonaceous mudstone, representing a swamp facies, overlies the channel sediments and includes taxodiaceous conifers and riparian trees. The mudstone units on top of the swamp facies also contain taxodiaceous conifers and riparian trees, but also have preserved a record of the aquatic and understory vegetation. Hoffman & Stockey (1999) interpret these as reflecting deposition in the distal margin of a crevasse splay. Units above the mudstone coarsen upward and are nearly devoid of fossils except for a zone of articulated fish skeletons. The sequences reflecting channel-abandonment, the swamp horizon, and the base of the crevasse splay have yielded the best assemblages of plant fossils.

The Joffre Bridge Roadcut locality is the most floristically diverse of the Paskapoo Formation floras with over 28 species named (Hoffman 2002). The dominant plant in this flora is by far *Joffrea speirsae*, an extinct member of the Cercidiphyllaceae. *Joffrea* has been reconstructed as a “whole plant”, based on interconnected organs including inflorescences, infructescences, seeds, pollen and leaves, as well as young seedlings (Stockey & Crane 1983; Crane & Stockey 1985, 1986a). A second whole plant reconstruction is of the “Joffre Plane Tree”, a platanaceous plant based on leaves, pistillate inflorescences and infructescences (*Macginicarpa manchesteri*), staminate inflorescences, dispersed stamen clusters and in situ pollen (*Platananthus speirsae*), and young seedlings (Pigg & Stockey 1991). Other important taxa are the conifers *Glyptostrobus* and *Metasequoia* and leaves of *Beringiaphyllum* (Cornales). Other taxa include *Equisetum*, *Osmunda*, *Chaetoptelea*, *Averrhoites*, and *Acer*-like samaras.

Aquatic ferns (*e.g.*, *Azolla*), and monocots (*Limnobiophyllum*, *Pistia*) are prominent members of the floating vegetation. Other aquatic plants include the liverwort *Ricciopsis*. Structures referred to as “unidentified sheathing structures” are very similar to monocot “leaf rings” seen in abundance at Beicegel Creek (DeVore *et al.* 2004) and commonly throughout Paleocene strata. These leaf rings and associated leaves resemble the monocot leaf type *Zingiberopsis* (Hickey & Peterson 1978) whose affinities are unknown.

Case histories of Late Paleocene to Early Eocene plants

Filicalean ferns

Generally, filicalean ferns have not been studied in detail in late Paleocene to early Eocene localities of western North America. This is in part because they are not typically prominent components of the floras, and also because of the strong bias toward collecting and describing dicot leaves. Even with this sampling bias, however, there are several notable exceptions that may be related directly to the paleoecology of particular environments where ferns were prominent. Two examples are *Onoclea sensibilis* at Munce’s Hill, and the abundance of the fern association of *Woodwardia gravigida*, *Osmunda* and *Onoclea* in the Ravenscrag assemblage. Paleocene *Onoclea sensibilis* occupies essentially the same niche at Munce’s Hill, a wetland forest community, as it does today (Rothwell & Stockey 1991). In the Eocene, ferns are also locally important in several sites, including some of the Golden Valley floras.

In contrast is the surprising absence of ferns at the Almont locality and their relatively rare occurrence at Beicegel Creek where their record consists of fragmentary vegetative and fertile pinnules and anatomically preserved rhizomes (Pigg *et al.* 2006). To date, we have not been able to recognize whether this is preservational bias, or if indeed the ferns were not a major component of these floras. One potential explanation for this rarity of fern megafossils has to do with ground water levels and fluvial activity. This suggestion arises from consideration of the cycles documented for the Souris seam of the Ravenscrag Formation (Frank & Bend 2004). As noted above, the localities with significant records of ferns are found either in the Alberta Basin or northern edge of the Williston Basin. In regards to the Williston Basin in particular, the southern and western portions of the Basin are more strongly influenced by uplift events while more subsidence, in particular due to salt dissolution, is prevalent in the northern, Canadian region of the Basin. Higher-energy fluvial systems would, therefore probably prevail in the south and less energetic systems would be present in the Canadian portion of the Williston Basin. The cycles described by Frank & Bend (2004) occur in a low-energy fluvial plain. Of the six stages they documented there is a point during the second cycle where ferns persist as groundwater levels rise. However, Frank & Bend (2004) noticed, based on petrographic analysis of samples, an increase in clastics, indicating the migration of an active river channel towards the fern-dominated mire. Fluvial activity escalated to the point that detrital clastic material choked the fern-rich mire associated with peat formation. Possibly the higher energy regimes present in the Almont and Beicegel Creek systems exhibit a different cycle representative of higher energy river systems.

Azolla, *Salvinia* and other aquatics

The aquatic ferns *Azolla* and *Salvinia* are excellent indicators of still-water habitats and serve to document the presence of lacustrine environments. In general, there seems to be a replacement of *Azolla* by *Salvinia* across the Paleocene to Eocene transition in the Great Plains and Rocky Mountain regions. *Azolla* then reappears in the Eocene of the Bighorn Basin after the appearance of *Salvinia* (Table 4). Later in the Eocene, both taxa occur in the lake deposits of the Okanogan Highlands, where *Azolla* is especially common in some horizons (e.g., Arnold 1955, DeVore & Pigg 2008).

Several of the localities have diverse aquatic assemblages that include not only heterosporous water ferns but also *Isoetes*, monocots assignable to Araceae and Lemnaceae, and forms close to *Trapa*. At Ravenscrag, all of these components occur, and at Joffre Bridge we see *Azolla*, *Spirodela* and *Limnobiophyllum*, and possibly *Isoetes* (Table 4). *Isoetes* also occurs in the Golden Valley, Beicegel Creek and Wannagan Creek floras but not at Almont. Interestingly, although we see nymphaeaceous seeds at Almont (*Nuphar* and *Susiea*, a form in the *Eurale* lineage; Taylor *et al.* 2006), none of the other aquatics are present. The enigmatic *Porosia* (Manchester 2002b) is known in the Williston Basin and lower sections of the Bighorn Basin. *Typha* apparently comes in during the Eocene.

Studies of the Paleocene-Eocene transition in North America have largely focused on terrestrial ecosystems and their response to climate change. To date, we could not identify a study focused on the response of freshwater aquatic ecosystems across the Paleocene-Eocene transition. Such a study would require identifying stratigraphic sequences with facies containing assemblages of aquatics that have not been transported a significant distance from the site of deposition.

Ginkgo

Ginkgo is one of the most common genera found in the Almont flora and in certain sites within the Beicegel Creek locality and Wannagan Creek. It is rare in the Ravenscrag flora and at Joffre Bridge, and apparently absent at the Golden Valley and the Green River sites (Table 4). By the Eocene, the genus disappears in the Williston Basin, yet persists in the Bighorn Basin, and still remains present in northwestern North America into the Miocene. The record of *Ginkgo* at Almont is particularly interesting because in addition to well-preserved leaves, often with cuticle, numerous seeds and reproductive stalks also have been found (Crane *et al.* 1990). In some cases the fleshy sarcotesta of the seed is preserved. Even though *Ginkgo* leaves are rela-

tively common in many younger western Tertiary floras, the occurrence of seeds is rare.

Extant *Ginkgo* trees only become reproductively mature and capable of bearing seeds at 20–30 years of age (He *et al.* 1997). Because no natural populations of the genus are known, it is not clear what the extant plant's natural habitat would be, however, in the Cretaceous and Tertiary record, fossil *Ginkgo* is typically found in depositional environments that indicate open canopy forests in disturbed habitats, along stream margins and the distal sides of levees. There they commonly co-occur with riparian trees such as *Cercidiphyllum* and *Platanus* (Royer *et al.* 2003). At Almont *Ginkgo* co-occurs with these taxa, along with other genera, and the depositional environment is inferred to be a meandering fluvial system. What is unusual is the occurrence of numerous *Ginkgo* seeds and reproductive stalks. If fossil *Ginkgos* shared the phenology of today's forms, this suggests that the ginkgos at Almont were mature forest trees. Why *Ginkgo* seeds are well preserved at Almont and not at similar localities, is unclear.

Taxodiaceous conifers

Although taxodiaceous conifers (*Taxodium*, *Parataxodium*, *Metasequoia* and *Glyptostrobus*) are common components of the Paleocene to Early Eocene floras of western North America, their actual patterns of distribution are interesting. *Taxodium* and *Parataxodium* are present at Genesee, early parts of the Williston Basin (Almont, Beicegel Creek and Wannagan Creek) and early in the Bighorn Basin. *Metasequoia* is common in most areas, except for Almont and Beicegel Creek, and is only in the early Green River floras. This genus is particularly significant at the Munce's Hill locality in Alberta, where a whole plant reconstruction of *Metasequoia foxii* includes different developmental stages of seedlings (Falder *et al.* 1999, Stockey *et al.* 2001). *Glyptostrobus* is widespread throughout the Bighorn Basin and appears sporadically in other sites, at Ravenscrag, in Alberta, at both Golden Valley sites and Wannagan Creek, and rarely at Almont. Hoffman & Stockey (1999) note that at Joffre Bridge these conifers dominate the "mollusc layer" which is interpreted as a swamp horizon. Today, *Taxodium* is limited in its natural distribution to the southeastern United States, while *Metasequoia* and *Glyptostrobus* are Asian. It seems that in the examined floras *Taxodium*-like plant remains are less common, except at Almont, providing another example of Almont's unusual flora in comparison to other Paleocene sites. We note that pines (not recorded in Table 4) are quite rare in the late Paleocene and early Eocene of the Great Plains and Rocky Mountains.

Table 4. Qualitative distribution of important Paleocene and Early-Middle Eocene taxa in western North America. Older names are included in parentheses after current identifications. Localities and floras: Bighorn Basin (BH; ages a–j); Green River (GR; ages a–g); in the Williston Basin: Almont (al), Beicegel Creek (bc), Golden Valley (gv), Bear Den Member (bd), Camels Butte Member (cb), Wannagan Creek (wc), Ravenscrag (rv); in the Alberta Basin (AB): Genesee (ge), Joffre Bridge (jb), Munce’s Hill (mh). + present, – absent, C – common, R – rare, VC – very common, * most common taxon at locality. Locality details for Green River and Bighorn Basins are detailed in Table 5. Based on literature cited in the text and personal observations.

Taxon	BH abcdefghij	GR abcdefg	WB al	WB bc	WB gv(bd)	WB gv(cb)	WB wc	WB rv	AB ge	AB mh	AB jb
Pteridophytes											
<i>Azolla</i>	hij	–	–	–	–	–	+	+	+	–	+
<i>Salvinia</i>	fghij	def	–	–	–	–	–	–	–	–	–
<i>Lygodium</i>	fj	def	–	–	–	+	–	–	–	–	–
<i>Onoclea</i>	a	–	–	–	+	+	–	+	–	+	–
<i>Osmunda macrophylla</i>	–	a	–	–	+	–	–	+R	–	–	–
<i>Woodwardia gravida</i>	defj	be	–	+	+	–	–	+C	–	–	–
<i>Equisetum</i>	abdfgj	abefg	–	–	+	–	+	+	–	+	+R
<i>Isoetes horridus</i>	e	–	–	+	–	+	+	+	–	–	+
Gymnosperms											
<i>Ginkgo</i>	abefgh	–	+C	+C	–	–	+	+R	–	–	+R
<i>Zamia coloradensis</i>	d	–	–	–	–	–	–	–	–	–	–
<i>Fokienia</i>	abde	–	–	–	–	–	–	+R	+	–	–
<i>Glyptostrobus</i>	abcdefgj	be	+R	–	+	+	+	+	+	–	+
<i>Metasequoia</i>	abcdefgh	abd	+	–	+	+	–	+R	+	+*	+
<i>Taxodium /Parataxodium</i>	ab	?	+	+	–	–	+	–	+	–	–
Angiosperms											
Betulaceae											
<i>Betula/Corylites</i>	de	abc	+VC	+VC	–	+	–	–	–	+	–
<i>Palaeocarpinus</i>	+	ab	+	+	–	–	–	–	–	+	–
Celtidaceae											
<i>Celtis aspera (Viburnum asperum)</i>	acde	ab	–	–	–	–	+	–	–	–	–
Cercidiphyllaceae											
<i>Cercidiphyllum/Joffrea</i>	abcdefghj	ab	+	–	+	+	+	+	+	+R	+*
<i>Nyssidium</i>	–	?	+	–	+	–	–	+	–	–	+
Cornaceae											
<i>Cornus</i>	def	–	+	+	+	+	–	+	–	–	–
Lemnaceae											
<i>Limnobiophyllum (Spirodela)</i>	hi	–	–	–	–	–	–	+	–	–	+
Nyssaceae											
<i>Browniea (Dicotylophyllum anomalum)</i>	a	+?	+R	—	+	+	+	+*	?	?	?
<i>Davidia (Viburnum antiquum)</i>	cd	ab	+	+	+	+	+	–	–	–	–
<i>Beringiaphyllum (Viburnum cupanioides)</i>	bcde	ab	+	+	+	–	+	–	–	–	+
Platanaceae											
<i>Platanus raynoldsii</i>	abcdefghj	ag	–	–	–	–	+	–	–	–	–
Sapindaceae											
<i>Aesculus hickeyi (Carya antiquorum)</i>	abcdef	abc	+	–	*	–	+	–	–	–	–
Tochodendraceae											
<i>Zizyphoides (Cocculus flabella)</i>	a	?	+C	+VC	+	+	+	–	–	–	–
Incertae sedis											
<i>Averrhoites</i>	abcdefghj	bcdefg	+	–	+	+	–	+	–	–	+
<i>Porosia</i>	bcde	b	+	+	+	–	–	+	–	–	–
<i>Zingiberopsis isonervosa</i>	deghij	bcdef	+R	+	–	+	+	+	–	–	+

Table 5. Locality information for Bighorn Basin and Green River Basin data used in Table 4. Localities are listed from oldest (a) to youngest (j). Bighorn Basin localities refer to numerous (1–40) sites; Green River localities are listed by name. See Wing *et al.* (1995) and Wilf (2000) for details.

Bighorn Basin				Mean richness of facies types			
Localities	No. sites	NALMA	Formation	backswamp	alluvial ridge	channel	pond
a	7	Puercan	Fort Union	6	9	6	–
b	4	Torrejonian	Fort Union	11	11	3	–
c	8	Tiffanian	Fort Union	–	9.3	3	–
d	11	E Clarkforkian	Fort Union	13.1	15.5	–	–
e	7	L Clarkforkian	Fort Union	11.7	–	–	16
f	33	E Graybullian	Fort Union	8.9	11.4	3	–
g	7	M Graybullian	Fort Union	7	–	–	16.5
h	5	L Graybullian	Fort Union	–	–	–	14.7
i	1	Lysitian	Wasatch	–	–	–	38
j	40	Lostcabinian	Wasatch	10.6	–	2	–

Green River Basin						
Localities	Listed as	No. sites	NALMA	Formation	Facies type	
Bison Basin	a	14	Tiffanian	Fort Union	alluvial	
Clarkforkian Big Multi	b	49 & 15	Clarkforkian	upper Fort Union–lower Wasatch	alluvial	
Wasatch Main Body	c	6	Graybullian-Lysitian	upper Fort Union	alluvial	
Latham	d	7	Lysitian	Wasatch–Ranger Ranch	alluvial	
Sourdough	e	31	E Lostcabinian	Wasatch–upper Ranger Ranch	alluvial	
Niland Tongue	f	5	Lostcabinian	Wasatch	alluvial	
Little Mountain	g	3	E Bridgerian	Green River	lacustrine	

Cercidiphyllaceae and Trochodendraceae

The families Cercidiphyllaceae and Trochodendraceae are today endemic to Asia, but both have a widespread fossil record in the Tertiary of the Northern Hemisphere. Vegetative leaves of Cercidiphyllaceae have been variously referred to *Cercidiphyllum* and *Trochodendroides*, and infructescences to *Nyssidium* (McIver & Basinger 1993, Crane *et al.* 1990), while the whole plant reconstruction of the extinct genus *Joffrea* has demonstrated additional variability in the fossil record (Stockey & Crane 1983; Crane & Stockey 1985, 1986a). In the Trochodendraceae, leaves referred to as *Zizyphoides*, *Cocculus*, and a variety of other names, are found in association with the distinctive fruits of *Nordenskiodia* and these fossil remains generally are accepted as representing an extinct member of the Trochodendraceae (Crane *et al.* 1991, but see Doweld 1998).

These leaf and fruit types all occur in Paleocene and Eocene localities, however the two families tend to be mutually exclusive of one another. Cercidiphyllaceae taxa are common at Ravenscrag, Golden Valley, Wannagan Creek, early Green River, throughout the Bighorn Basin and at the Alberta sites (dominant at Joffre

Bridge; Hoffman & Stockey 1999) and rare at Almont (Table 4). *Zizyphoides* leaves are present in the Williston Basin (common at Almont and Beicegel Creek) and present only in the earliest Bighorn Basin site. Although there has been some confusion in distinguishing these leaf forms, this pattern of one taxon being present at a given site in the absence of the other appears to have some basis. One possible explanation is that the *Joffrea* and *Nordenskiodia* plants occupied similar niches. By chance, the first species that dispersed in new, favorable habitats would become established in the community and prevent the second species from becoming a major component of the flora.

Palaeocarpinus

Fossil betulaceous leaves, often placed in the genera *Betula* or *Corylites*, are common components of many Paleocene-to-Eocene floras in western North America (Table 4). While some Eocene forms (*e.g.*, *Betula leopoldae* of western Canada) are known with reproductive structures characteristic of true *Betula* (*e.g.*, Crane & Stockey 1986b), those of the Paleocene of North America

and Asia are frequently found in association with *Palaeocarpinus*, a mosaic taxon with a combination of features seen in *Corylus* and *Carpinus* today. Three different species of *Palaeocarpinus* are known in the Paleocene of western North America: *P. joffrensis* from Munce's Hill; *P. dakotensis* from Almont and Beicegel Creek; and *P. aspinosa* from Wyoming. While this genus disappears in the Rockies and Great Basin by the end of the Paleocene, additional species of *Palaeocarpinus* are known in the Eocene of the Pacific Northwest and Far East Russia (Manchester *et al.* 2004).

Conclusions

In this paper we have presented an analysis of the major floras of the late Paleocene to early Eocene transition in North America in the context of their depositional environments. This transition is well documented in the western Rocky Mountains and the Western Interior of North America in several well-defined basins. In contrast, in eastern North America it is more difficult to define because floras of these ages are rare, and the deposition of time transgressive stratigraphic units often cannot be definitively dated.

Each of the western basins that form the basis of this paper is tectonically defined and has its own distinctive and discernable history. The paleoenvironmental conditions within each basin are the agents responsible for sampling the flora, and understanding the mode in which they do this is critical to understanding the composition of the resulting flora. For example, not all basins are dominated by large lakes; in some basins there is a wide range of fluvial and lacustrine depositional settings (Table 2). In the case of exceptionally preserved floras (*e.g.*, Almont), an unusual set of preservational conditions provide the morphological and anatomical data for high resolution systematic context. Together these factors provide the basis for understanding the late Paleocene-early Eocene floral record and its relationships with European floras.

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