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Reconstructing the environment of the northern Rocky Mountains during the Eocene/Oligocene transition: constraints from the palaeobotany and geology of south-western Montana, USA

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ABSTRACT. The fossil floras of south-western Montana, U.S.A. contain an important record of climate and biotic change in the northern Rocky Mountains across the Eocene/Oligocene transition. Palaeogene climate and biotic evolution in the northern Rocky Mountains is poorly known compared to central/southern Rocky Mountains (Florissant) and Pacific coast (Bridge Creek) localities even though this area is of critical importance as a Palaeogene ecotone between the central Rocky Mountains and Pacific coast regions and between contemporary high and low elevation vegetation. Statistical analysis of fossil leaf morphology and the distribution of plant taxa at the family level were used to estimate palaeoclimate parameters and to determine nearest living analogs for the palaeofloral associations of southwestern Montana. Palaeoclimate estimates indicate moderate cooling and a pronounced summer drying trend associated with the establishment of widespread Antarctic glaciation in the early Oligocene. The taxonomic structure of the floras of southwestern Montana changed from warm temperate/subtropical taxa to warm/cool temperate taxa including a pronounced xeric (dry-adapted) component across the Eocene/Oligocene transition. Early Oligocene palaeoelevation estimates vary from ~ 2.5 km in the east to ~ 1.5 km in the west coincident with a previously interpreted Palaeogene rift valley system.

KEYWORDS: Palaeoclimate, Palaeoelevation, Palaeofloral evolution, Multivariable statistics, Eocene/Oligocene transition, Montana

INTRODUCTION

The period encompassing middle Eocene to early Oligocene time was a critical transition period for terrestrial climate and biotic evolution. This era witnessed the gradual deterioration of worldwide greenhouse conditions and the slow stepwise cooling and drying of the global climate culminating in the full continental glaciation of Antarctica and the beginning of global icehouse conditions during the early Oligocene (Prother 1994, Zachos et al. 2001, Ivany et al. 2006). In North America, Palaeogene climate shifts were accompanied by profound regional changes in terrestrial vegetation and dependent biological systems (Wing 1987, Graham 1998 & 2011). In the Pacific Northwest, a late Eocene (~38.5 Ma) cooling event resulted in the replacement of evergreen subtropical vegetation by temperate deciduous forest (Myers 2003). Mesothermal conditions returned briefly in the latest Eocene (~37 Ma) but the long term cooling trend continued across the Eocene/Oligocene boundary (Myers 2003). Throughout the interior Pacific Northwest, modest cooling (~ 2–3°C), increased rainfall seasonality and a reduction in the cold month mean temperature are observed across the Eocene/Oligocene boundary (Graham 1999, Myers 2003). In response to these climate trends, cool temperate vegetation migrated coastward and toward lower elevations (Wolfe 1992a, Myers 2003, Graham 2011).

In the central and southern Rocky Mountains, a similar cooling and drying trend is observed. The warm temperate to subtropical latest Eocene (34.1 Ma) Florissant flora of Colorado gave way to the cool temperate early Oligocene Antero flora (Graham 1999, Meyer 2003). The younger Oligocene (~27 Ma) Creede flora is representative of modern Rocky Mountain high altitude coniferous forest (Meyer, 2003). These vegetation shifts indicate a change in mean annual temperature from 12–14°C at Florissant to 0–6°C at Creede (Meyer 2003).

The late Eocene/early Oligocene palaeofloras of southwestern Montana occupy a geographic position between the Pacific coast and central Rocky Mountains and contain many taxa identical or closely related to species from both these areas. However, the relationship between climate and floral change in the northern Rockies is poorly understood compared to the better studied palaeofloras of Colorado and the Pacific Northwest. Moreover, southwestern Montana during the Palaeogene was divided into many semi-isolated basins separated by significant highlands (Lielke 2012, Rothfuss et al. 2012, Lielke & Thomas 2012a, b) resulting in the juxtaposition of high and low elevation vegetation. Therefore, the palaeofloras of southwestern Montana are an important link connecting Pacific coast and continental interior ecosystems as well as illustrating the dynamics of altitudinal zonation of Palaeogene vegetation.

FOSSIL FLORAS OF SOUTHWEST MONTANA

Fossil plants in southwestern Montana, U.S.A. are found in the lacustrine, fluvial and paludal sediments of the Palaeogene Renova and Medicine Lodge Formations (Fig. 1). Although the same sequence of strata is not present in every basin (Fig. 2), age determinations from biostratigraphy, magnetostratigraphy and radiometric dating (Tabrum et al. 1997, Tabrum et al. 2002, Fritz et al. 2007) suggest a predominance of late Eocene and early Oligocene sediments (Chadronian, Orellan and Whitneyan North American land mammal ages (NALMA)). Biostratigraphy and magnetostratigraphy from the Sage Creek area east of Dell, Montana indicate that the Eocene-Oligocene (E/O) transition is locally preserved in the Palaeogene sediments of southwestern Montana (Tabrum et al. 1997).

In southwestern Montana, two areas in particular host abundant, well-studied palaeobotanical remains – the Fossil Basin area in the Upper Ruby River Valley (Becker 1960, 1961, 1964, 1972 1973) and the Beaverhead Basins area west of Clark Canyon Reservoir (Becker 1964 1969). The Fossil Basin area contains four palaeofloras located at different stratigraphic levels all within a small area of only a few km^2. These are, in order of decreasing age, the Mormon Creek, Metzel Ranch, Ruby and York Ranch palaeofloras. The Beaverhead Basins fossil material was subdivided by Becker (1969) into three units – in order of decreasing age, the Christensen Ranch, Horse Prairie and Medicine Lodge floras located in three small areas each separated by about ten kilometers.

These seven palaeofloras appear to straddle the E/O transition and therefore provide critical constraints on Palaeogene climatic and biotic change in the North American continental interior. In the Fossil Basin area, the oldest assemblage, the Mormon Creek flora, occurs in fluvial overbank mudstone of the Climbing Arrow Member of the Renova Formation. Lithologically identical mudstones at this stratigraphic level in the Climbing Arrow Member contain early Chadronian NALMA fossils (late Eocene) at localities to the north and south of the Fossil Basin area (Monroe 1976, 1981). Given its stratigraphic position, the Mormon Creek palaeoflora likely predates the final climatic deterioration at the E/O boundary. The Metzel Ranch flora occurs in lithologically similar mudstones near the top of the Climbing Arrow Member, stratigraphically close to the lacustrine shales which house the Ruby flora. Previously, the Ruby laminated shales were wrongly assigned to the early Miocene Passamari Member of the Renova Formation (Monroe 1976). This improper age assignment led earlier authors to wrongly conclude that the Ruby flora was the youngest of the four Fossil Basin palaeofloras (Wing 1987, Graham 1998, 2011).

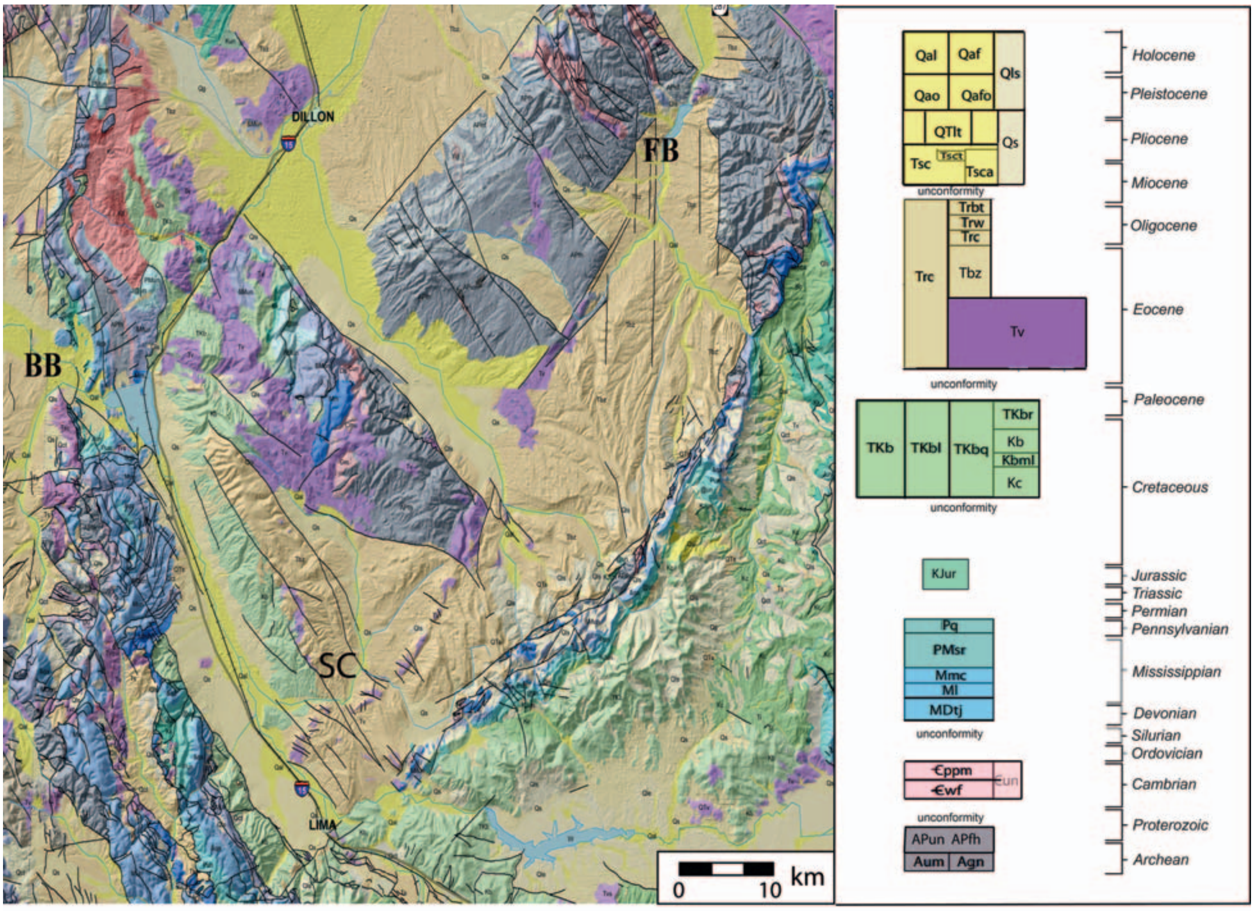

Fig. 1. Geologic map of southwestern Montana, USA. Bold faced letters indicate fossil plant localities – **BB** = Beaverhead Basins area west of Clark Canyon Reservoir, **SC** = Sage Creek Basin & **FB** = Fossil Basin locality in the Upper Ruby River Valley (Modified from Portner, 2003). Eocene/Oligocene aged strata are light brown/tan on this map and Paleogene volcanics are purple

Recent radiometric age dating and magnetostratigraphic studies have led to revisions in the age of several regional floras (notably the Florissant and Bridge Creek floras) with close affinities to the Montana palaeofloras and to changes in the correlation of NALMA with the standard geologic time scale. Becker (1960, 1961) based his original age assignments on correlations with allied fossil floras now considered late Eocene/early Oligocene, rather than late Oligocene/early Miocene, in age (Meyer & Manchester 1997, Meyer 2003) and on associated Chadronian mammal fossils, then considered Oligocene, and now correlated with the late Eocene (Prothero 1985, 1994, 1995, Lloyd et al. 2008).

Based on these revised ages and new field observations, the Ruby laminated shales and similar sediments to the north and northeast are reassigned to the top of the late Eocene/early Oligocene Climbing Arrow Member (Lielke 2012, Lielke & Thomas 2012a). Following these age revisions, the Metzel Ranch and Ruby floras are reinterpreted as a transitional phase of vegetation close to the E/O boundary. The York Ranch flora occurs within fluvial sandstone of the Oligocene Dunbar Creek Member of the Renova Formation and clearly postdates the E/O boundary. In the Williams Creek area, several kilometers to the northeast, the Dunbar Creek Member is overlain by a 32.2 ± 0.4 Ma basalt flow (Petkewich 1972, Fritz et al. 2007) which provides an uppermost age constrain on the Fossil Basin palaeofloras.

In the Beaverhead Basins area, fossil mammal remains of Chadronian (late Eocene) age underlie the palaeobotanical sites which are in turn overlain by early Arikareean (late Oligocene) fossils (Matoush 2002). Basalt overlying the lacustrine deposits of the Medicine Lodge Formation has been dated at 27.5 ± 0.78 Ma, providing an uppermost boundary for the age of the palaeofloras (Janecke et al. 1999). The stratigraphic location of the palaeofloral sites combined with a high

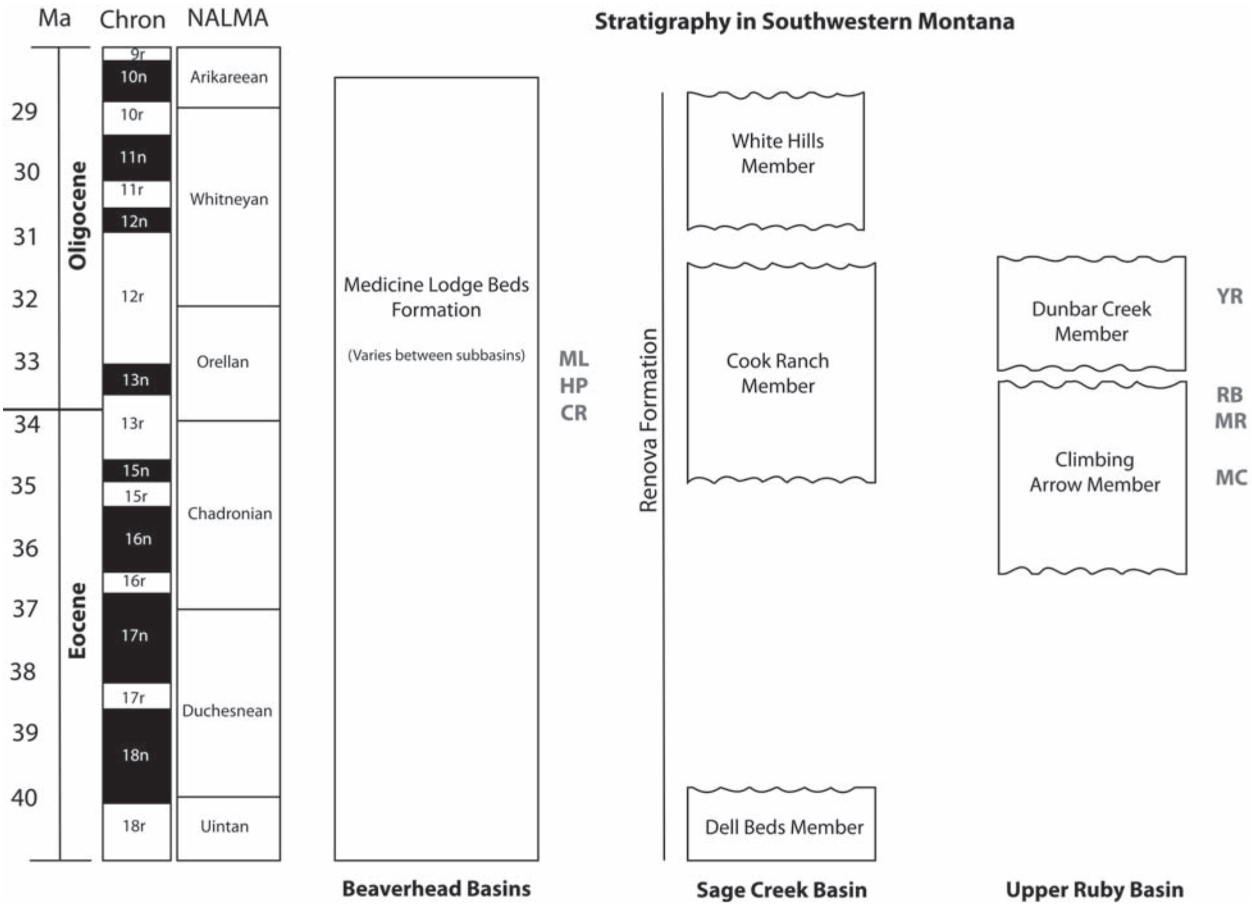

Fig. 2. Stratigraphy of the Paleogene Renova Formation and Medicine Lodge Beds Formation in southwestern Montana and eastern Idaho. Chronologic data included for absolute age (in million years (Ma)), geomagnetic polarity time scale (chrons) and North American Land Mammal Age (NALMA). The Sage Creek Basin is located approximately halfway between the Beaverhead Basins area and the upper Ruby River Valley. Letters indicate the approximate stratigraphic position of fossil floras – **ML** = Medicine Lodge paleoflora, **HP** = Horse Prairie paleoflora, **CR** = Christensen Ranch paleoflora, **YR** = York Ranch paleoflora, **RB** = Ruby paleoflora, **MR** = Metzel Ranch paleoflora and **MC** = Mormon Creek paleoflora

percentage (~40%) of shared species suggest that the Beaverhead Basins palaeofloras are early Oligocene, or less likely latest Eocene, transitional assemblages similar in age to the Ruby and Metzel Ranch floras (Becker 1969). Similarity coefficients calculated using plant family presence/absence data for each palaeoflora also suggest a close relationship to the Ruby and Metzel Ranch palaeofloras and less affiliation with the older Mormon Creek and younger York Ranch palaeofloras (Table 5).

REVISED PALAEOFLORA TAXA LISTS

The fossil floras of southwestern Montana were published as monographs by Herman Becker during the 1960's and 70's (Becker 1960, 1961, 1969, 1972, 1973) and have not been systematically reviewed since then. Recent work on Palaeogene palaeofloras from the central/southern Rocky Mountains and Pacific Northwest (especially the Florissant and Bridge Creek floras) suggest that the taxonomic assignments of the palaeofloras of southwestern Montana are in need of revision. A preliminary updated version of the Becker floral lists (Table 1) is presented here. This revision is based largely on work published since 1980 on similar and identical species from the Florissant and Bridge Creek floras (Meyer & Manchester 1997, Manchester 2001). However, a more thorough taxonomic revision, beyond the scope of the present study, is clearly still needed. These new floral lists were used to calculate nearest living analogs (NLA) for the southwestern Montana palaeofloras.

Table 1. Revised floral lists for gymnosperm and angiosperm taxa contained in the Fossil Basin and Beaverhead Basins paleofloras. These revisions are based on taxonomic work conducted on floras of comparable Paleogene age since the original publication of Hermann Becker's monographs on the fossil plants of southwestern Montana. In particular the latest Eocene Florissant (Meyer 2003, Manchester 2000) and early Oligocene Bridge Creek (Meyer & Manchester 1997) paleofloras contain affiliated taxa. New names are in **bold**, questionable assignments in the original Becker monographs are indicated by a preceeding *, names followed by a superscript ^{P} are taxa attested by pollen data as well as megafloral remains (pollen data from Leopold et al. (1973)). An **X** under the heading for each paleoflora indicates the presence of diagnostic megafloral remains while a **P** indicates taxa known only from palynomorph data. Superscript numerals indicate footnotes for taxa modified from Becker's original taxonomic assignments

Family	Genus	Species / Morphotypes	Mormon Creek	Metzel Ranch	Ruby	York Ranch	Beaver-Head Basins
Pinaceae	*Abies*^{P}	*laticarpa*			**X**		**X**
		alvordensis					**X**
		concoloroides					**X**
		longirostris			**X**		
	Picea^{P}	*lahontensis*			**X**		**X**
		magna					**X**
		sonomensis					**X**
	Pinus[1]^{P}	*florissanti*			**X**		**X**
		macginitiei			**X**		
		**monticolensis*			**X**		
		**hexaphylla*			**X**		
		**tetrafolia*			**X**		
		wheeleri					**X**
	Pseudolarix	*americana*					**X**
	Pseudotsuga^{P}	*masoni*			**X**		
		longifolia					**X**
		sonomensis					**X**
Taxaceae							**P**
Taxodiaceae^{P}	*Glyptostrobus*	*oregonensis*			**X**		**X**
		dakotensis	**X**				
	Metasequoia	*occidentalis*			**X**		**X**
	Sequoia^{P}	*affinis*				**X**	**X**
	Taxodium	*dubium*					**X**
Cupressaceae^{P}	*Chamaecyparis*	*linguaefolia*			**X**		**X**
	Juniperus	*nevadensis*		**X**			**X**
	Thuja	*diamorpha*		**X**			**X**
Gnetaceae	*Ephedra*	*sp.*					**P**
Ginkgoaceae	*Ginkgo*[2]	*adiantoides*		**X**	**X**		**X**
Typhaceae^{P}	*Typha*[3]	*lesquereuxi*		**X**	**X**	**X**	**X**
Gramineae	*Phragmites*	*alaskana*		**X**			
	Agrostis	*primaeva*					**X**
	Arundo	*pseudogoepperti*					**X**
	Poacites	*sp.*					**X**
Sabiaceae	***Sabia***[4]	*sp.*					**X**
Limnanthaceae	*Floerkea*	*rubyensis*			**X**		
Potamogetonaceae[5]	*Potamogeton*	*parvus*			**X**		
Cyperaceae	***Eleocharis***[6]	*lacustris*			**X**		
		angustifolius	**X**				
Liliaceae	**Smilax*[7]	*rubyensis*			**X**		
		trinervis					**X**
Cannaceae	*Canna*[8]	*flaccidafolia*					**X**
Salicaceae	*Populus*	*balsamoides*	**X**	**X**	**X**	**X**	**X**
		adamantea	**X**	**X**		**X**	
		cedrusensis				**X**	
		cinnamomoides		**X**			
		crassa			**X**		
		eotremuloides				**X**	
		lindgreni		**X**			
		payettensis				**X**	**X**

Table 1. Continued

Family	Genus	Species / Morphotypes	Mormon Creek	Metzel Ranch	Ruby	York Ranch	Beaver-Head Basins
Salicaceae	*Populus*	*salicoides*			**X**		
		succorensis					**X**
		washoensis				**X**	
	Psuedosalix[9]	*cockerelli*	**X**			**X**	
		longiacuminata				**X**	
		succorensis				**X**	**X**
	Salix	*coloradica*			**X**		
		hesperia		**X**		**X**	
		knowltoni		**X**			
		laevigatoides				**X**	
		longiacuminata				**X**	
		schimperi				**X**	
		stipulata				**X**	
		taxifolioides		**X**			
		truckeana		**X**		**X**	**X**
		wildcatensis					**X**
		wimmerianna		**X**		**X**	**X**
		longissima			**X**		
		rivularis			**X**		
Myricaceae	**Myrica*[10]	*dorfi*	**X**		**X**		
		lignitum	**X**	**X**			
		mormonensis	**X**	**X**			
		metzeli			**X**		
		serrulata		**X**	**X**		**X**
Juglandaceae	*Carya*[P]	*antiquorum*				**X**	
		libbeyi				**X**	**X**
	Engelhardtia	*sp.*					**P**
	Juglans	*sp.*				**X**	
Betulaceae	*Alnus*[P]	*carpinoides*			**X**		
		jarbidgana		**X**		**X**	
		protomaximowiczii					**X**
		relata			**X**	**X**	**X**
	Betula	*fairii*				**X**	**X**
		thor					**X**
		vera					**X**
		sp.			**X**		
	Paracarpinus[11]	*lanceolata*			**X**	**X**	
		fraterna				**X**	**X**
	Corylus	*insignis*					**X**
	**Ostrya*[12]	*oregoniana*					**X**
Fagaceae	*Fagus*	*washoensis*			**X**		
	Castanea	*spokanensis*		**X**		**X**	
		dolichophylla					**X**
		miomollissima					**X**
	Fagopsis[13]	*longifolia*			**X**		**X**
	Quercus[P]	*brooksi*			**X**		
		consimilis			**X**		
		convexa			**X**		**X**
		dayana					**X**
		dispersa				**X**	
		elwyni	**X**				
		eoprinus					**X**
		hannibali					**X**
		mohavensis			**X**		
		prelobata					**X**

Table 1. Continued

Family	Genus	Species / Morphotypes	Mormon Creek	Metzel Ranch	Ruby	York Ranch	Beaver-Head Basins
Fagaceae	*Quercus*[P]	*prevariabilis*					**X**
		pseudolryata					**X**
		simulata					**X**
		winstanleyi					**X**
Ulmaceae[P]	*Celtis*	*mccoshi*			**X**	**X**	
		alderensis	**X**				
		chaneyi				**X**	
		kansana		**X**			
	Ulmus[P]	*montanensis*			**X**	**X**	
		moorei		**X**			
		paucidentata			**X**		**X**
		speciosa			**X**	**X**	**X**
	Cedrelospermum[14P]	*drymeja*		**X**	**X**		**X**
		hesperia				**X**	
		nervosa	**X**			**X**	
		oregoniana		**X**	**X**		**X**
		ungeri					**X**
Moraceae	*Morus*	*symmetrica*			**X**		
		eorubra	**X**				
*Proteaceae[15]	**Lomatia*	*lineata*			**X**		
	**Knightophyllum*	*angustum*	**X**				
		wilcoxianum	**X**				
Eucommiaceae	*Eucommia*	*browni*			**X**		
Nymphaeaceae	*Nymphaeites*	*nevadensis*		**X**			**X**
	Nelumbo	*sp.*					**X**
	Nuphar	*advenoides*					**X**
Cercidiphyllaceae	**Cercidiphyllum*[16]	*elongatum*	**X**		**X**		**X**
		arcticum				**X**	**X**
		crenatum		**X**			
Ranunculaceae	*Clematis*	*ellensburgensis*					**X**
Berberidaceae	*Mahonia*	*marginata*			**X**		
		hakeaeformis	**X**				**X**
		limirivuli					**X**
		lobodonta					**X**
		obliqua			**X**		**X**
		reticulata					**X**
		simplex		**X**			**X**
		subdenticulata	**X**		**X**		**X**
		peloronta			**X**		
	Berberis	*acanthoides*					**X**
Cruciferae	*Thlaspi*	*primaevum*			**X**		
Saxifragaceae	*Philadelphus*	*parvulus*			**X**		
	**Hydrangea*	*knowltoni*		**X**			**X**
		californica	**X**				
	Ribes	*auratum*			**X**		
		cerinum			**X**		
Eucommiaceae	*Eucommia*	*montana*		**X**			**X**
Menispermaceae	*Cocculus*	*heteromorpha*					**X**
Lauraceae	*Laurophyllum*	*intermedium*	**X**				
	Nectandra	*antillanafolia*	**X**				
	Persea	*praelingus*	**X**				
	**Sassafras*[17]	*ashleyi*				**X**	
		columbiana					**X**
		hesperia				**X**	
Elaeagnaceae	*Eleagnus*	*sp.*					**P**

Table 1. Continued

Family	Genus	Species / Morphotypes	Mormon Creek	Metzel Ranch	Ruby	York Ranch	Beaver-Head Basins
Hamamelidaceae	*Exbucklandia*	*oregonensis*				**X**	
Platanaceae	*Platanus*	*dissecta*		**X**			**X**
		stenoloba					**X**
Rosaceae[P]	*Cercocarpus*[18]	*antiquus*			**X**		**X**
		bea-annae			**X**		**X**
		myricaefolius					**X**
	Amelanchier	*dignata*	**X**				
		couleeana					**X**
		covea					**X**
	Chamaebatia	*prefoliolosa*			**X**		
	**Crataegus*[19]	*copeana*			**X**		
		elwyni		**X**			
		pacifica					**X**
	Kerria	*antiqua*					**X**
	**Potentilla*[20]	*passamariensis*			**X**		
		horkelioides					**X**
		salmonensis			**X**		**X**
	Prunus	*scottii*	**X**	**X**		**X**	
		lyoniifolia				**X**	
		moragensis				**X**	
		wilcoxiana				**X**	
	Pyracantha	*spatulata*				**X**	
	Rosa	*hilliae*		**X**	**X**	**X**	**X**
	Sorbus	*carcharodonta*			**X**		
		harneyensis		**X**			
	Spiraea	*clavidens*			**X**	**X**	
		decurrens		**X**			
	Vauquelinia	*coloradensis*					**X**
	Waldsteinia	*insolita*			**X**		
Leguminosae[21]	*Leguminosites*	*sp.*			**X**		
	Albizzia	*ovalicarpa*	**X**				
	Caesalpinites	*acuminatus*					**X**
		coloradicus					**X**
	Canavalia	*eocenica*					**X**
	Cassia	*glenni*	**X**				
		fayettensis					**X**
		hesperia					**X**
		reticuloides					**X**
	Cercis	*parvifolia*		**X**			**X**
		spokanensis				**X**	
	Cladrastis	*oregonensis*					**X**
		prelutea					**X**
	Conzattia	*coriaceae*					**X**
	Dalbergia	*retusa*					**X**
	Desmodium	*rubycanum*	**X**				
	Diphysa	*presuberosa*					**X**
	Leucaena	*californica*		**X**			**X**
	Lonchocarpus	*oregonensis*	**X**				
	Mimosites	*acaciafolius*					**X**
	Parkinsonia	*constricta*					**X**
	Pithecolobium	*eocenicum*					**X**
	Robinia	*californica*					**X**
		lesquereuxi					**X**
	Sophora	*spokanensis*		**X**			
	Astragalus	*wilmattae*			**X**		

Table 1. Continued

Family	Genus	Species / Morphotypes	Mormon Creek	Metzel Ranch	Ruby	York Ranch	Beaver-Head Basins
Simaroubaceae	*Ailanthus*	*americana*		**X**	**X**		**X**
	Chaneya[22]	*truncatum*			**X**		**X**
Meliaceae	**Cedrela*[23]	*lancifolia*			**X**		**X**
		pteraformis		**X**			**X**
Anacardiaceae	*Cotinus*	*fraterna*			**X**		
	Metopium	*metopioides*					**X**
	Rhus	*obscura*		**X**			**X**
		milleri				**X**	
		miosuccedanea					**X**
		praeovata				**X**	
		stellariaefolia		**X**			
Euphorbiaceae[P]	*Mallotus*	*riparius*	**X**				
Aquifoliaceae	*Ilex*	*acuminata*	**X**				
		rubyensis	**X**				
Celastraceae	*Celastrinites*	*populoides*	**X**				
	Celastrophyllum	*antrorsum*	**X**				
	Celastrus	*robertsi*	**X**				
		typicus					**X**
	Euonymus	*pacificus*					**X**
Staphyleaceae	*Staphylea*	*splendens*	**X**				
Sapindaceae[24]	*Acer*	*florissanti*			**X**		
		**aequidentatum*	**X**				
		**bendirei*					**X**
		bolanderi					**X**
		**glabroides*		**X**	**X**	**X**	**X**
		**minor*		**X**			**X**
		**oregonianum*					**X**
		**scottiae*					**X**
	Athyana	*haydeni*					**X**
	**Cardiospermum*[25]	*terminale*			**X**		**X**
	Cupanites	*formosus*	**X**				
	Dipteronia	*insignis*		**X**	**X**		**X**
	**Dodonaea*[26]	*reniptera*			**X**		
	**Koelreuteria*[27]	*arnoldi*			**X**		**X**
		bipinnatoides		**X**			
		mixta	**X**				
		nigricans	**X**				
	**Sapindus*[28]	*coloradensis*		**X**	**X**		**X**
Rhamnaceae	*Berchemia*	*huanoides*					**X**
	Ceanothus	*variabilis*		**X**			
		prespinosus					**X**
	Colubrina	*pre-elliptica*					**X**
	Paliurus	*dumosus*					**X**
		florissanti		**X**	**X**		
	Reynosia	*preanuntia*					**X**
	Rhamnus	*rubyvallis*		**X**			
		crocea				**X**	
	Rhamnites	*berchemiaformis*	**X**				
		psuedo-stenophyllus					**X**
	Rhaemnus	*plena*	**X**				
Vitaceae	*Vitis*	*muscadinioides*		**X**	**X**	**X**	
		washingtonensis				**X**	
Nyssaceae	*Nyssa*	*crenata*			**X**	**X**	
		hesperia		**X**			

Table 1. Continued

Family	Genus	Species / Morphotypes	Mormon Creek	Metzel Ranch	Ruby	York Ranch	Beaver-Head Basins
Elaeocarpaceae	*Elaeocarpus*	*apiminax*	**X**				
Alangiaceae	*Alangium*	*aequalifolium*		**X**			**X**
	Grewiopsis	*elegans*	**X**				
Ericaceae	*Vaccinium*	*sophoroides*		**X**			**X**
	Arctostaphylos	*cuneata*					**X**
Dilleniaceae	*Dillenites*	*tetracerafolia*	**X**				
Flacourtiaceae	*Idesia*	*glandulosa*	**X**				
Eleagnaceae	*Shepherdia*	*weaveri*	**X**				
Araliaceae	*Aralia*	*rubyensis*	**X**				
		taurinensis	**X**				
Cornaceae	*Cornus*	*buchi*	**X**				
		cornella			**X**		**X**
		ovalis		**X**		**X**	
	Alangium	*aequalifolium*					**X**
Sapotaceae	*Bumelia*	*balli*	**X**				
Ebenaceae	*Diospyros*[29]	*oregoniana*					**X**
Oleaceae	*Fraxinus*	*rupinarum*		**X**	**X**		**X**
		brevialata					**X**
		eocenica	**X**				
		flexifolia					**X**
		yubaensis	**X**				
	Osmanthus	*preamissa*					**X**
Malvaceae[30P]	***Craigia***[31]	*cassioides*			**X**		
		miocenica	**X**				**X**
	Florissantia[32]	*speiri*			**X**		**X**
	**Sterculia*	*wilcoxensis*					**X**
	Tilia	*inaequalis*				**X**	
		aspera					**X**
Caprifoliaceae	*Symphoricarpus*	*elegans*			**X**		
	Sambucus	*newtoni*					**X**
	**Viburnum*[33]	*palmatum*		**X**			
		kraeuseli					**X**
Scrophulariaceae	*Paulownia*	*columbiana*				**X**	
		thomsoni					**X**
Bignoniaceae	*Catalpa*	*rubyensis*				**X**	
	Callichlamys	*zeteki*	**X**				
*Compositae[34]	*Viguiera*	*cronquisti*					**X**

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[1] Following reassessment of Florissant pines, the foliage and seeds (pl. 8, figs 1–4, Becker 1961) & (pl. 6, figs 1, 2, Becker 1969) previously assigned to *P. florissanti* reassigned to *P. macginitei*, cones (pl. 8, figs 5, 9, Becker 1961) & (pl. 9, fig. 12, Becker 1961) may still be valid as *P. florissanti*. Four to six (mostly 5) needle fasicles previously assigned to *P. monticolensis*, *P. tetrafolia & P. hexaphylla* likely *P. wheeleri*. *P. tetrafolia & P. hexaphylla* were defined on the basis of single specimens and are more likely unusual specimens of *P. wheeleri* rather than new species.

[2] Several short shoots (pl. 5, fig. 1, Becker 1969) & (pl. 1, fig. 6, Becker 1972) are questionably aligned with *Ginkgo* and may instead belong to *Pseudolarix* or another gymnosperm genus. However, the presence of a single *Ginkgo* leaf (fig. 4, Becker 1964) establishes the presence of the Ginkgoaceae in the Ruby paper shale flora.

[3] Some specimens interpreted as *Typha* leaves are rejected based on the absence of wavy cross veins between the primary veins (pl. 13, figs 13–18, Becker 1969). However, other leaves may still be legitimate *Typha* (pl. 2, fig. 6, Becker 1972), Pollen establishes the presence of the family Typhaceae in the Beaverhead Basins flora (Leopold & MacGinitie, 1972).

[4] These fruits (formerly *Symplocarpus* (pl. 13, figs 19, 20, Becker 1969)) are provisionally reassigned to *Sabia* (Sabiaceae), The family Araceae is likely not present based on current specimens.

[5] Formerly family Zosteraceae

[6] Formerly genus Cyperacites

[7] Entire margin leaves in Ruby flora (pl. 11, figs 9–11, Becker 1961) could be *Dioscorea* instead. Similar shaped leaves with toothed margins in Beaverhead Basins (pl. 15, fig. 7, Becker 1969) are likely Rhamnaceae (*Paliurus*, *Ceanothus*).

[8] Possibly *Zingiberales* rather than *Canna*.

[9] *Psuedosalix* recognized by Manchester (2006) includes *Salix cockerelli*, *S. longiacuminata & S. succorensis* (leaves) *Antholithes botryantra & A. tulipoidea* (fruits) and *Carpites carum-carvi & C. eludens* (capsules). Other species of *Populus* and *Salix* could properly belong in *Pseudosalix* as well. Given the known variability of leaves of the Salicaceae, several of Becker's established

species could be invalid especially if based on only a few specimens. Some reproductive axes previously assigned to *Populus* (pl. 16, figs 7, 8, Becker 1969) are likely taxodiaceous pollen cones instead.

[10] Some specimens assigned to *Myrica* (pl. 16, figs 16, 17, Becker 1969) may be Rosaceae instead based on details of the compound teeth.

[11] *Carpinus* specimens reassigned to extinct genus *Paracarpinus*. *Asterocarpinus* fruits are also present in Beaverhead Basins flora (Manchester & Crane, 1987).

[12] Assignment to *Ostrya* questionable. Venation (pl. 18, fig. 7, Becker 1969) suggests that inclusion in Rosaceae is more likely.

[13] Following Manchester & Crane (1983), the extinct genus *Fagopsis* has been moved from the Betulaceae to the Fagaceae.

[14] As at Florissant, *Zelkova* leaves have been reassigned to *Cedrelospermum* (Manchester,1989) although the distinctive *Cedrelospermum* fruits have not been found in SW Montana to date. *Zelkova* could still be present in Montana although macrofossil evidence for its occurrence is equivical. Pollen assigned to *Zelkova* was reported by (Leopold & MacGinitie, 1972).

[15] The southern hemisphere family Proteaceae is not considered valid at contemporary North American Paleogene localities. The proper assignment of these genera is unknown.

[16] Leaves assigned to *Cercidiphyllum* (pl. 24, figs 5, 7, Becker 1969) reassigned to extinct genus *Trochodendroides*, pods (pl. 24, fig., Becker 1969) reassigned to extinct genus *Nyssidium*.

[17] Some specimens assigned to *Sassafras* (pl. 26, figs 8–10, Becker 1969) and (pl. 25, figs 5–8, Becker 1973) may be *Lindera* or *Litsea* instead.

[18] Species identified as *Cercocarpus* (pl. 22, figs 1–6, Becker 1961) and (pl. 30, figs 13–21, Becker 1969) may represent an extinct ancestral genus rather than the extant genus *Cercocarpus*.

[19] Assignment to *Crataegus* questionable.

[20] Some specimens assigned to *Potentilla* (pl. 30, figs 1–5, Becker 1969) and (pl. 22, figs 18–21, Becker 1961) may be *Rosa* instead. Specimens lacking distinctive characters provisionally retained in *Potentilla*.

[21] Assignment of speciemns of Leguminosae to genera are provisional as these specimens often lack distinguishing characters which would allow identification to the generic level. Some pods assigned to *Cercis* (pl. 32, fig. 8, Becker 1969) are not *Cercis* owing to the lack of a wing along the suture.

[22] Fruits (pl. 34, figs 5–12, Becker 1969) and (pl. 25, figs 1, 2 Becker 1961) originally assigned to *Astronium* (Anacardiaceae) now belong to the extinct genus *Chaneya* (Simaroubaceae). Leaves (pl. 34, fig. 4, Becker 1969) may belong to *Rhus*

[23] Seeds could be *Toona* instead.

[24] Family Aceraceae now considered to be a subfamily of family Sapindaceae. Fossil Acer was extensively revised by Wolfe & Tanai (1987). These revisions are summarized as follows (see Wolfe and Tanai (1987) for details and specimen numbers): Only *A. florissanti* and possibly *A. bolanderi* are still considered valid, *A. aequidentatum* is reassigned to *Platanus appendiculata* & *A. bendirei* is reassigned to *Platanus bendirei*, *A. glabroides*, *A. minor*, *A. oregonium* & *A. scottiae* are considered invalid. Specimens assigned to these four species are reassigned to *A. alverdense*, *A. beckeri*, *A. elwyni*, *A. grantense*, *A. hueberi*, *A. macginitiei*, *A. montanense* & *A.* tiffneyi

[25] Questionable assignment to *Cardiospermum*. Most likely an extinct genus of Sapindaceae.

[26] No collaboration of *Dodonea* from distinctive winged seeds.

[27] No collaboration of *Koelreuteria* from distinctive fruit valves.

[28] Evidence for affiliation with genus *Sapindus* equivical.

[29] *Diospyros* fruits (pl. 38, figs 2–22, Becker 1969) are reassigned to *Paliurus*. Leaves are undiagnostic for *Diospyros* so the presence of the family Ebenaceae cannot be substantiated.

[30] The families Steruliaceae, Tiliaceae & Bombacaceae now combined into Malvaceae. Specimen assigned to *Sterculia* (pl. 38, fig. 3, 1969) more likely *Platanus*.

[31] Fruits originally assigned to *Ptelia* (pl. 33, figs 7–14, Becker 1969), (pl. 10, figs 12–14, Becker 1972) and (pl. 23, figs 16–18, Becker 1961) in the family Rutaceae are reassigned to *Craigia* in the family Mavaceae.

[32] Specimens formerly assigned to *Holmskioldia* (pl. 30, figs 1–3, Becker 1961) and (pl. 39, figs 6, 7, Becker 1969) in the family Verbenaceae now assigned to extinct genus *Florissantia* in Malvaceae.

[33] Specimens previously assigned to *Viburnum* (pl. 39, fig. 11, Becker 1969) likely belong to family Platanaceae instead. *Viburnum* cannot be substantiated.

[34] No distinctive features assign this specimen (pl. 39, fig. 15, Becker 1969) to Compositae. It is more likely a degraded cuppresaceous cone. Compositae cannot be substantiated

RATIONALE OF STUDY METHODOLOGY

Previous methods for estimating palaeoclimate from fossil plant remains fall under two basic categories: 1) methods based on a nearest living analog (NLA) for the taxa under investigation, and 2) those based on the morphology of fossil leaves and the known empirical relations between modern leaf characters and the physical environment (Givnish 1979, 1986, Graham 1998). The earliest estimates of palaeoclimate either involved finding the nearest living relatives of individual fossil species and assigning similar climatic tolerances to their ancestors (MacGinitie 1953), or employed the strong correlation between mean annual temperature (MAT) and the presence of entire leaf margins (Wolfe 1979), which was first established by Bailey and Sinnott (1915, 1916). More recent attempts at palaeoenvironmental reconstruction have generally employed multiple linear regression (MLR) and ordination techniques to establish empirical relationships between multiple (> 30) leaf characters and modern climate variables (Wing & Greenwood 1993, Wolfe 1993, Gregory & McIntosh

1996, Wiemann et al. 1998). These empirical relationships are then used to estimate palaeoclimate from fossil leaf characters. Ordination techniques have also been used to establish modern analogs for palaeofloral associations (Boyle et al. 2008).

The datasets available for palaeobotanical analysis have also evolved over time. The original Climate Leaf Analysis Multivariate Program (CLAMP) dataset of Wolfe (1993), which has served as the foundation for most published MLR models, was based on 106 modern sites and 29 leaf characters (see Table 2). The number of modern sites and leaf characters has increased over time and the version of the CLAMP dataset used in this study (referred to here as CLAMP-173) employs 33 character states and 173 modern sites (*http://www.open.ac.uk/earth-research/spicer/CLAMP*).

This expanded dataset was used in part to address the lack of sites with winter frost conditions in the earlier data set. Although

Table 2. Coefficients for new multi-variable linear regression equations developed from the CLAMP-173 dataset. Also included are new single variable linear equations for selected climate parameters. Correlation coefficients (R2) and standard errors are included for each paleoclimate equation

	New MLR equation coefficients								
	MAT	WMMT	CMMT	GROW-SEAS	GSP	MMGSP	3-WET	3-DRY	ENTHAL
Intercept	12.846	40.089	–4.522	6.029	–13.475	–11.125	–18.557	–39.664	27.059
Lobed			0.195	0.052					0.015
No Teeth	0.157	–0.121	0.213	0.064					0.061
Regular teeth	–0.080	–0.035				0.089			
Close teeth			–0.063	–0.036					
Round teeth		–0.193		–0.025	–1.206	–0.123	–0.460	–0.221	0.016
Acute teeth	0.051				–1.133		–0.113	0.466	0.017
Compound teeth		–0.294		–0.006					
Nanophyll		0.192			–2.314	–0.110	–0.806		
Leptophyll 1			–0.153		0.566				–0.023
Leptophyll 2	–0.161	–0.143			–1.581				–0.021
Microphyll 1									
Microphyll 2									
Microphyll 3									
Mesophyll 1			0.093	0.081	0.330				
Mesophyll 2			0.274		0.430		0.477	–0.931	0.039
Mesophyll 3		–0.172				0.128		0.513	
Emarginate apex	0.082	0.035	0.160	0.022					0.026
Round apex									
Acute apex									
Attenuate apex					1.701	0.193	0.896	0.512	0.008
Cordate base		0.132		0.033					
Round base	–0.045								–0.010
Acute base									
L:W <1:1	–0.219	–0.165	–0.419	–0.173	–0.822	–0.129	–0.631		–0.043
L:W 1–2:1									
L:W 2–3:1					1.715	0.161	0.520	0.345	
L:W 3–4:1					3.822	0.423	1.775	0.788	–0.020
L:W >4:1									
Obovate									
Elliptic					1.500	0.228	0.754	0.638	0.009
Ovate				0.005					
R squared (R^2)	0.884	0.795	0.854	0.863	0.787	0.783	0.786	0.771	0.885
Standard error (±)	2.371	2.498	3.605	1.188	42.455	4.415	17.545	11.581	0.509

New single linear regression (SLR) equations

MAT = .275 (No Teeth) + 1.34 $R^2 = .775$
WMMT = .182 (No Teeth) + 14.37 $R^2 = .551$
CMMT = .360 (No Teeth) – 10.99 $R^2 = .727$
GROWSEAS = .124 (No Teeth) + 2.29 $R^2 = .748$
3-DRY = 1.08 (Atten Apex) + .004 $R^2 = .610$
3-WET = 1.54 (Atten Apex) + 10.61 $R^2 = .507$

probably not a major source of error when dealing with pre-middle Eocene palaeofloras (Wing & Greenwood 1993), this bias towards sites with frost free winters is an increasing liability when dealing with late Eocene transitional and post-Eocene icehouse palaeofloras. The CLAMP-173 dataset was used to develop new single & multiple linear regression (SLR & MLR) equations better suited to post-Middle Eocene climates with cold winter conditions. These equations were then used to estimate palaeoclimate parameters for Palaeogene Montana. Leaf physiognomy scores for the Montana palaeofloras were based mainly on the published descriptions of Becker (1960, 1961, 1964, 1969, 1972, 1973) supplemented by new specimens collected during the period 2008–2010 and archived at the University of Montana Palaeontology Center.

In order to compare changes in climate with changes in the taxonomic structure of ancient plant communities, nearest living analogs (NLA) were determined by using a statistical measure of similarity (the Gower similarity coefficient) to match each palaeoflora with its ten closest modern analogs. The Alwyn Gentry forest transect database of plant diversity for 226 modern sites was used to provide NLA for the Montana palaeofloras (Phillips & Miller 2002). Trends in the associations of fossil taxa were also examined if these trends represent either important structural changes (the elimination of subtropical and East Asian endemic lineages) or have particular climatic significance (the appearance of dry-adapted, or xeric, taxa).

Two fundamental problems are inherent in the reconstruction of ancient climate and ecosystem dynamics from fossil remains: 1) fossil assemblages do not present a completely accurate picture of past ecosystems due to differential fossilization and preservation potential, and 2) due to biological evolution and extinction, organisms in the past may have either left no descendent lineages which can provide a modern analog for their ancestors' climatic and habitat preferences, or the descendent lineages could have changed their environmental tolerances over time.

One way to minimize the impact of these problems is to incorporate multiple independent lines of investigation and see if they converge on a consistent interpretation of past environmental conditions. It is also desirable to analyze biological features which result from the basic physiological requirements of the organisms under investigation, and which therefore are not easily changed by natural selection (Givnish 1979). Examination of higher taxa (genera and families) minimize these problems as higher order taxonomic units are slower to accumulate evolutionary changes and are based on more fundamental biological characteristics than individual species (Boyle et al. 2008). They are also less prone to misidentification – a particular problem when dealing with lineages containing few extant species or those with a limited modern distribution (Boyle et al. 2008). Because of these considerations, presence /absence data for plant families was used exclusively to determine nearest living analogs (NLA).

STATISTICAL PROCEDURES

Equations for climatic parameters were determined by first subjecting the CLAMP-173 dataset to Canonical Correspondence Analysis (CCA) using the *GINKGO* multivariate analysis software – a program of the VegAna (Vegetation Edition and Analysis) package, developed by the Department of Vegetal Biology of the University of Barcelona (*http://biodiver.bio.ub.es/vegana*), designed primarily for the ordination and classification of modern ecological data (Ainsa 2005, Bouxin 2005). CCA is a constrained ordination technique which is essentially a hybrid of ordination and multiple linear regression (McGarigal et al., 2000). Its purpose is to extract the major gradients in a dependent dataset (in this case leaf characters) that can be accounted for by a set of independent explanatory variables (in this case climate parameters) and that are assumed to have a causal link (McGarigal et al. 2000, Ainsa 2005). The ability of CCA to constrain the ordination of a set of dependent variables with a set of independent explanatory variables is an advantage over unconstrained ordination techniques such as Principal Component Analysis (PCA) which assesses the relationships within a single set of interdependent variables without attempting to define causal relationships with independent variables outside the original dataset (McGarigal et al. 2000).

Following Wolfe (1993, 1995) and Gregory and McIntosh (1996), the results of the

CCA analysis were used to determine thand leaf characters most closely related to each climatic parameter of interest. However, in order to estimate palaeoclimate parameters, the CLAMP method of projecting palaeofloral leaf character values onto CCA climate vectors was not employed here. Following Wing and Greenwood (1993) and Wiemann et al. (1998), multiple linear regression (MLR) analysis was performed using the CAA results as guideposts to maximize the statistical significance of the MLR models. Since CCA ordination axes are the linear combinations of explanatory variables which account for most of the variation in the dependent variables, CCA is a useful tool for determining which leaf characters have the highest correlation with each climatic parameter. CCA is also not hampered by multicollinearity or high correlations between dependent or independent variables (McGarigal et al. 2000).

The multiple regression analysis tool available as an add-on for Microsoft EXCEL spreadsheet software was used to calculate single and multiple linear regression (SLR & MLR) equations relating each climate variable to the leaf characters most closely associated with it, as determined from CCA analysis. Summary statistics for each of these equations are provided in Appendix 1. Values for the leaf characters of the Montana palaeofloras, scored according to the CLAMP methodology, were then inserted into each equation to estimate the value and standard error of each palaeoclimatic variable. Single variable equations were also determined for comparison with MLR equations and to provide a tool for estimating climate parameters for fossil sites that haven't been scored following the full CLAMP methodology, or for reconnaissance surveys.

In order to examine the relations between the Montana palaeofloras, other regional palaeofloras and modern forest sites, several measures of statistical similarity were tested in order to determine the technique which provided the most useful ordering of the various datasets. The Gower similarity coefficient, contained within the *GINKGO* program, was chosen since it is applicable to qualitative binary data (i.e. plant family presence-absence), qualitative data composed of more than two states, and quantitative data (i.e. leaf character percentages) or any combination of these data types (Dunn & Everitt 1982) thereby providing a single statistical measure for all the data included in this study. Exploratory testing confirmed that the Gower coefficient provided the most meaningful division of the CLAMP and Gentry datasets. As a complement to the above techniques, principle component analysis (PCA) also was used to identify the major ecological gradients and other trends present within the plant taxa, leaf character and climate data and to calculate the Euclidean distance between fossil and modern sites (Ainsa 2005).

POTENTIAL BIASES AND SOURCES OF ERROR

No method of reconstructing ancient environments, especially quantitatively, is immune from error. Biases associated with the methods employed here fall into two basic categories, 1) bias inherent in the data, and 2) bias associated with the statistical techniques employed. Since it was first proposed, the utility of the CLAMP database as a basis for palaeoclimate reconstruction has been called into question. Wilf (1997) argued that the multiple character states employed by CLAMP primarily serve to multiply error rather than increase the precision of climate estimates. Some specific sources of potential error within the CLAMP database have also been proposed. Peppe et al. (2010) pointed out that the CLAMP database appears to have a systematic bias regarding leaf size, making climate estimates based on CLAMP subject to potentially large, difficult to quantify, errors.

Because of the incompleteness of the fossil record, evolutionary change and the impossibility of directly measuring past environmental variables, no statistical analysis of proxy data will completely avoid sampling bias or remove the effects of the interdependence of explanatory variables. The approach advocated here is to look for similar trends within multiple lines of independent evidence when reconstructing past environments. Observed climate trends, for example increasing seasonality, are considered to be valid if they are corroborated by data from independent geologic or palaeontological sources.

In order to evaluate the influence of bias on the results of this study, climate estimates from representative, previously published multiple linear regression (MLR) equations were examined along with mean climate values from the five best nearest living analog sites (Gentry dataset) for each palaeoflora site. Modern climate data were acquired from United States federal and state government internet databases (http://www.ncdc.noaa.gov/oa/ncdc.html).

Fossil Basin palaeoclimate estimates from this study and from published multiple linear regression models, along with the averaged climate data from NLA sites, are plotted in Figure 3 for mean annual temperature (MAT) and growing season precipitation (GSP).

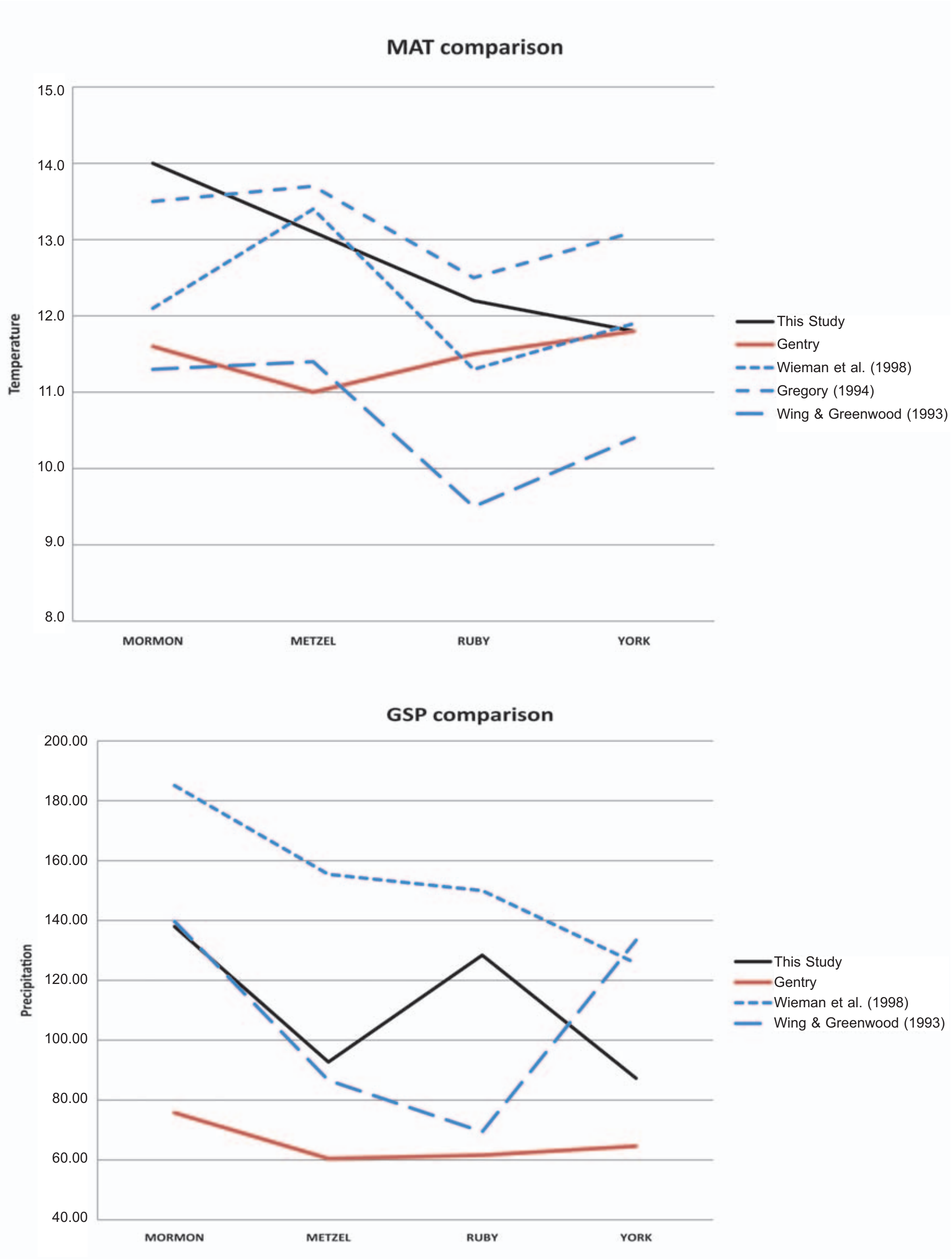

Fig. 3. Comparison of Mean Annual Temperature (MAT) and Growing Season Precipitation (GSP) from equations derived from multiple linear regression models and the CLAMP dataset and from nearest living analog models. Black line = paleoclimate estimates from this study, blue lines = paleoclimate estimates from previously published multiple linear regression models, and red line = paleoclimate estimates derived from nearest living analog sites in the Gentry database

Comparison of MLR results with the results of nearest living analog (NLA) climate averages, a palaeoclimate proxy entirely independent of the CLAMP dataset and leaf physiognomy analysis, indicates general agreement with the interpretation of the Oligocene Fossil Basin locality as a cool, dry temperate environment. Estimates from NLA also show a MAT and GSP decline between the time of deposition of the Mormon Creek and the Metzel Ranch floras in agreement with the results of this study. However, estimates based on NLA have a relatively low resolution since there are a limited number of temperate analog sites, most with similar climate parameters, in the Gentry database. Moreover, modern ecosystems and climate are not necessarily representative of ancient ecosystems and climate – all ancient sites are, strictly speaking, non analog sites. However, when considered in the context of independent corroborating evidence, NLA estimates can serve as useful first order estimates of ancient climate and as an important check on the results of leaf physiognomy or stable isotopic analysis.

Palaeoclimate estimates based on leaf physiognomy show broad correspondence with each other although some important differences are apparent. Estimates from previously published MAT equations (which employ earlier versions of CLAMP with fewer sites) are basically cyclical as opposed to the linear decrease found in this study. Palaeotemperature differences may be due to the over-representation of sites with frost free winters in earlier versions of CLAMP. Equations based on earlier CLAMP data give little weight to any leaf characters except entire margins and the length/width ratio – the wider range of leaf margin characters seen in temperate toothed species is therefore under-represented in models based on earlier CLAMP data.

Estimates for growing season precipitation from previously published equations show a greater range of variability than MAT estimates. Wiemann et al. (1998) GSP estimates show a similar cyclical pattern but higher overall precipitation compared to GSP estimates from this study. Wing & Greenwood (1993) GSP estimates are virtually identical to those from this study for the Mormon Creek and Metzel Ranch floras but show opposite trends for the Ruby and York Ranch floras. Equations for GSP from this study and from Wiemann et al. (1998) place more weight on small leaf size and type of leaf margin and less weight on the length/width ratio compared to the Wing and Greenwood (1993) equation. This may account for the different results observed with the Ruby flora, characterized by small leaf size, and the York Ranch flora, which contains the largest leaf specimens of any of the Fossil Basin palaeofloras.

FOSSIL BASIN PALAEOFLORAS

PALAEOCLIMATE ESTIMATES

New palaeoclimate estimates from the Fossil Basin palaeofloras show several clear trends with important implications for the Eocene-Oligocene climate record in the western continental interior of North America (Fig. 4). The overall trend in mean annual temperature (MAT) was a steady decline of ~2.25°C from late Eocene to early Oligocene time accompanied by a relatively small overall decline in warm and cold month mean temperatures (WMMT & CMMT). Seasonality, as indicated by the difference between WMMT and CMMT, was high with estimates for WMMT in particular higher than values calculated from previously published equations. Although it is possible that these new equations may overestimate WMMT, new estimates for MAT and CMMT are similar to those calculated from previously published equations. The presence of a distinct xeric (dry-adapted) component in the Ruby and Metzel Ranch floras and associated geologic and palaeontological evidence, such as the presence of land tortoises and gypsum (Monroe 1976), support the existence of a distinct dry season. Early Oligocene summer temperatures may have been enhanced by higher atmospheric CO_2 content during the Palaeogene (Arthur et al. 1991, Freeman & Hayes 1992, Pearson & Palmer 2000, Fletcher et al. 2007, Doria et al. 2011).

As opposed to estimates for temperature parameters, new estimates for precipitation parameters are basically cyclical (Fig. 5), possibly the result of moderate Antarctic glaciations in the late Eocene and more severe glacial conditions during the Oligocene (Zachos et al. 1992). If this is true, then Palaeogene Antarctic glaciation under conditions of higher atmospheric CO_2 content primarily influenced precipitation in the western continental interior with only minor temperature changes. However, one clear unidirectional trend, with important implications for the evolution of northern Rocky Mountains vegetation, is the permanent sharp decline of ~40 cm in three driest month's precipitation (3DRY) between the time of the Mormon Creek palaeoflora and the Metzel Ranch palaeoflora. The beginning of a pronounced summer dry season coincides with a fundamental shift in the taxonomic structure of the Fossil Basin palaeofloras as described in more detail below.

NEAREST LIVING ANALOGS

The Gentry dataset of modern plant taxa diversity (Phillips & Miller, 2002) was used to determine the nearest living analogs (NLA) for the fossil floras of southwestern Montana using the Gower similarity measure. These results are summarized in Tab. 3. The NLA for the three younger palaeofloras (Metzel Ranch, Ruby and York Ranch) are predominately from east-central North America (Missouri, Ohio and Indiana) with smaller contributions from the American east coast and Europe. These localities are predominately warm temperate dry forest following the Holdridge classification scheme (Phillips & Miller 2002). Since the Gentry dataset lacks sites representative of Rocky Mountain coniferous forest, NLA representing cold temperate moist and boreal wet Holdridge zones are interpreted as proxies for high elevation conifer-dominated vegetation incorporated into lacustrine host rocks. The existence of an ancestral Rocky Mountain Montane forest association during the Palaeogene is strongly supported by the middle Eocene Thunder Mountain flora of Idaho (Axelrod 1998) and the Republic flora of northeast Washington (Wolfe & Wehr 1987, Graham 1998, 2011).

The Mormon Creek flora is significantly different from the other three Fossil Basin palaeofloras in its taxonomic composition. It contains a smaller warm temperate component (split evenly between East Asian/European and eastern North American NLA sites) and a significant subtropical and high elevation

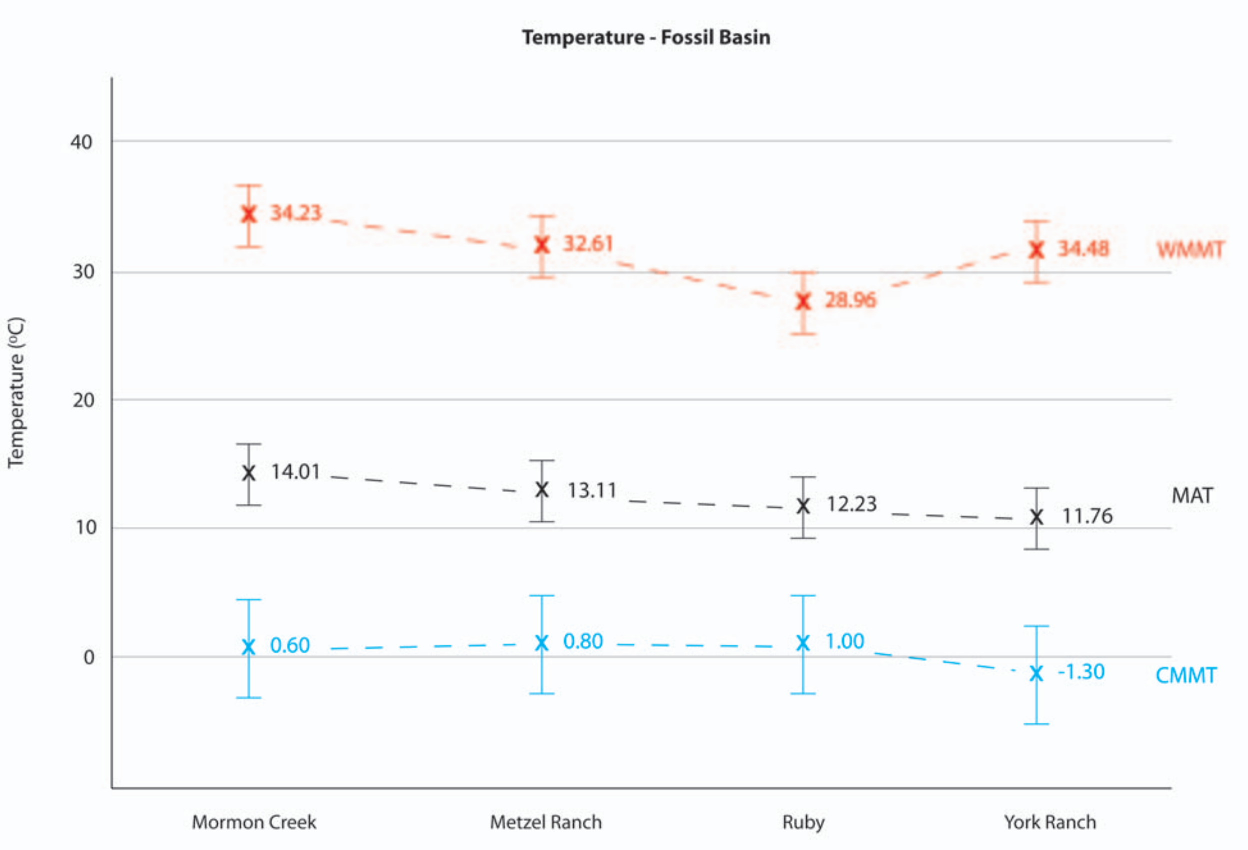

Fig. 4. New paleotemperature estimates for the Fossil Basin paleofloras. WMMT = warm month mean temperature, MAT = mean annual temperature, and CMMT = cold month mean temperature. Standard errors are: ±2.5°C for WMMT, ±2.4°C for MAT and ±3.6°C for CMMT

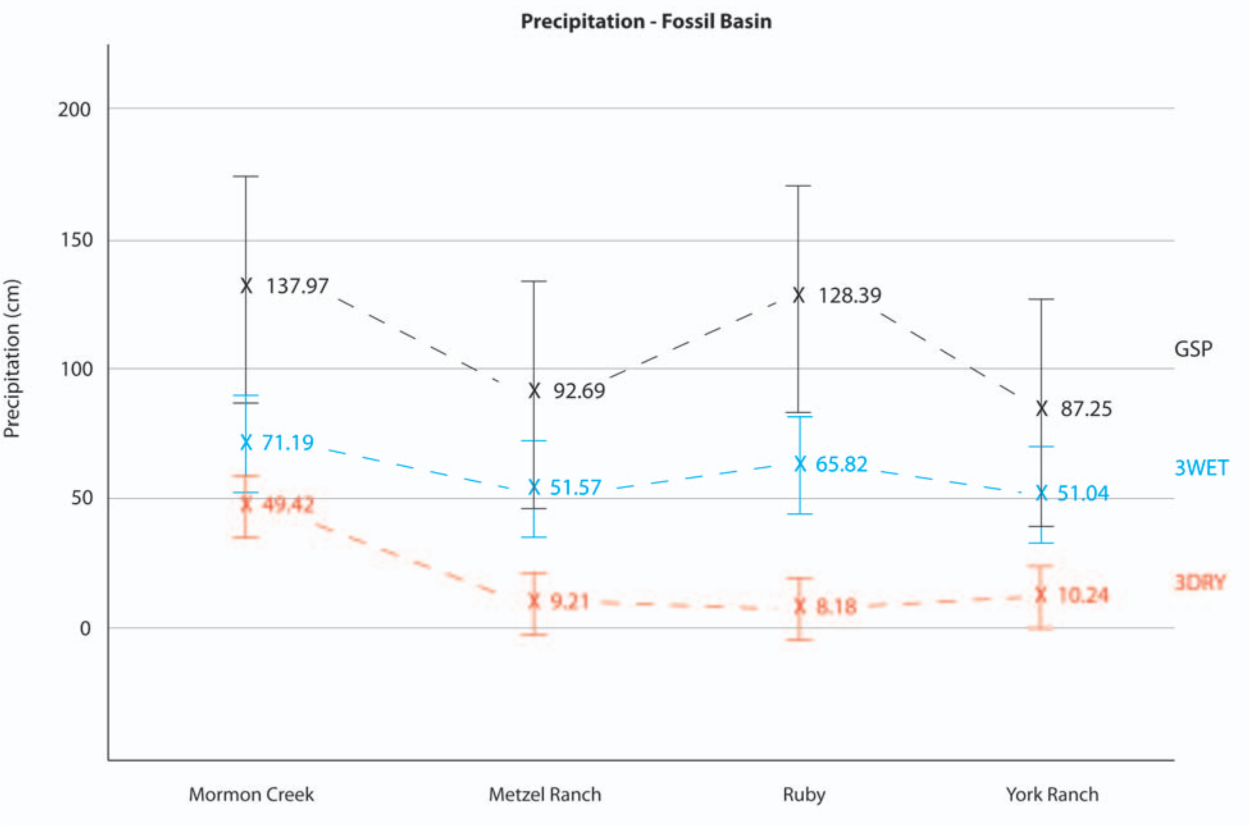

Fig. 5. New paleoprecipitation estimates for the Fossil Basin paleofloras. GSP = growing season precipitation, 3WET = precipitation for the three wettest months and 3DRY = precipitation for the three driest months. Standard errors are: ±42.5 cm for GSP, ±17.5 cm for 3WET and ±11.6 cm for 3DRY

tropical (East Asian and Central American) component not seen in the younger floras. Terrestrial gastropod faunas from southwestern Montana also indicate an Eocene warm temperate to subtropical climate with high summer month precipitation which became cooler, wetter and more temperate over time (Roth 1986). Similarly, on the West Coast, the E/O boundary event resulted in the widespread replacement of subtropical evergreen broad-leaved vegetation by deciduous broad-leaved vegetation dominated by diverse cool temperate lineages (Meyer 2003). Leopold and MacGinitie (1972), utilizing affinities at the species level, also reported a shift in temperate floral composition between the time of preservation of the Mormon Creek and Ruby floras, from primarily Old World temperate and pan-temperate species to species with New World temperate affinities.

The elimination of the Mormon Creek subtropical component coincides with the sharp decline in three driest months' precipitation (3DRY) between the time of deposition of the Mormon Creek and Metzel Ranch floras. Declines are also seen in growing season precipitation (GSP), mean month GSP (MMGSP) and three wettest months' precipitation (3WET) during this time frame. It is hypothesized that these precipitation declines, and especially the permanent decline in 3DRY precipitation, are responsible for the observed shift in taxonomic composition of the Fossil Basin palaeofloras. A parallel exists between this event and the early Eocene shift from palaeotropical to neotropical dominated plant communities. The main climate trend associated with this 'great schism' was also the development of seasonal rainfall (in the early Eocene case drier winters) and a decrease in total annual rainfall (Leopold & MacGinitie 1972).

Principal Component Analysis (PCA) was performed for both the CLAMP and Gentry datasets (including fossil sites in the ordinations) and analogs were determined by calculating the Euclidean distance between each site (Tab. 4). These results largely confirm the previous conclusions with the added result that the Fossil Basin palaeofloras show close affinities with East Asian temperate (mostly Japanese) localities in the CLAMP dataset. Under-representation of East Asian temperate localities in nearest living analogs calculated

Table 3. Holdridge life zones for nearest living analogs (NLA) from the Alwyn Gentry dataset (Phillips & Miller (2002)). Note wider variety of life zones represented within the Eocene Mormon Creek Flora as opposed to the Oligocene icehouse floras of the Metzel Ranch, Ruby, York Ranch and Beaverhead Basins paleofloras

	Mormon	Metzel	Ruby	York	Christensen	Horse Prairie	Medicine Lodge
1	Chiba (Japan)	Cuivre (Missouri)	Cuivre (Missouri)	Bankamp (Ohio)	Uppsala (Sweden)	Valleyvi (Missouri)	Rockcree (Missouri)
2	Quinceoc (Mexico)	Bankamp (Ohio)	Bankamp (Ohio)	Potomac (Virginia)	Ruissalo (Finland)	Rockcree (Missouri)	Cuivre (Missouri)
3	Valleyvi (Missouri)	Tysongla (Missouri)	Tysonwoo (Missouri)	Tysonwoo (Missouri)	Rockcree (Missouri)	Cuivre (Missouri)	Bankamp (Ohio)
4	Suderhac (Germany)	Valleyvi (Missouri)	Bablersp (Missouri)	Rockcree (Missouri)	Allacher (Germany)	Cedarblu (Indiana)	Valleyvi (Missouri)
5	Genting (Malaysia)	Heustomf (Ohio)	Tysongla (Missouri)	Cuivre (Missouri)	Valleyvi (Missouri)	Allacher (Germany)	Cedarblu (Indiana)
6	Avalanch (India)	Rockcree (Missouri)	Allacher (Germany)	Tysongla (Missouri)	Suderhac (Germany)	Montgome (New York)	Montgome (New York)
7	Sierraro (Cuba)	Tysonwoo (Missouri)	Heustomf (Ohio)	Cedarblu (Indiana)	Cary (New York)	Potomac (Virginia)	Tysonwoo (Missouri)
8	Campinas (Brazil)	Cedarblu (Indiana)	Valleyvi (Missouri)	Valleyvi (Missouri)	Kanealle (Pennsylvania)	Bablersp (Missouri)	Ruissalo (Finland)
9	Persever (Bolivia)	Bablersp (Missouri)	Rockcree (Missouri)	Indianca (Nebraska)	Cuivre (Missouri)	Bankamp (Ohio)	Wildbasi (Texas)
10	Bablersp (Missouri)	Wildbasi (Texas)	Ruissalo (Finland)	Ufhortic (Florida)	Cedarblu (Indiana)	Heustobm (Ohio)	Heustomf (Ohio)
Holdridge Life Zone							
Tropical Lower Montane Moist	2						
Tropical Premontane Wet	1						
Subtropical Moist	1						
Subtropical Montane Moist	1						
Subtropical Wet	1						
Warm Temperate Wet	1						
Warm Temperate Montane Wet					1		
Warm Temperate Moist		3	2	3	2	3	3
Warm Temperate Montane Moist		1					1
Warm Temperate Dry	2	6	6	7	2	5	4
Cool Temperate Moist	1		1		3	2	1
Boreal Wet			1		2		1

Table 4. Nearest living analogs (NLA) for Fossil Basin paleofloras based on leaf physiognomy data and the CLAMP-173 database. NLA determined by principle component analysis (PCA) including fossil sites in the ordination as though they were modern sites characterized by calculated physiognomy scores. The Euclidean distance between every modern and fossil site was determined and the five closest modern sites to each fossil locality were established as the NLA sites

No.	Mormon	Metzel	Ruby	York
1	Kiyosumi, Honshu	Kiyosumi, Honshu	Yakusugi 1080 m, Yakushima	Amagi-toge, Honshu
2	Amagi-toge, Honshu	Amagi-toge, Honshu	Kiyosumi, Honshu	Umedaira, Honshu
3	Yakusugi 1080 m, Yakushima	Umedaira, Honshu	Arakawa Dam, Yakushima	Kiyosumi, Honshu
4	Umedaira, Honshu	Tatsuta-yama, Kyushu	Higane Shrine, Honshu	Battle Cr., Maryland
5	Battle Cr., Maryland	Yakusugi 1080 m, Yakushima	Tatsuta-yama, Kyushu	Kidogawa 2, Honshu
6	Tatsuta-yama, Kyushu	Yakusugi 800 m, Yakushima	Amagi-toge, Honshu	Arakawa Dam, Yakushima
7	Kidogawa 2, Honshu	Yakusugi 1350 m, Yakushima	Umedaira, Honshu	Yakusugi 800 m, Yakushima
8	Zozu-san, Shikoku	Arakawa Dam, Yakushima	Yakusugi 1350 m, Yakushima	Pt. Grenville, Washington
9	Nekko 2, Honshu	Kidogawa 2, Honshu	Battle Cr., Maryland	Troutdale, Oregon
10	Yakusugi 800 m, Yakushima	Battle Cr., Maryland	Wolf Cr., Colorado	Port Orford, Oregon

from the Gentry dataset are likely due to the small number of temperate East Asian sites and taxa in the Gentry dataset (Phillips & Miller 2002). This result highlights the importance of using multiple datasets and methodologies in interpreting ancient environments.

OTHER VEGETATION TRENDS

Several significant trends in the composition of the Fossil Basin palaeofloras are evident in addition to the elimination of Eocene subtropical taxa. The most important of these involve the elimination of East Asian endemic species, the elimination of characteristic late Eocene riparian species such as *Fagopsis longifolia* and their apparent replacement by members of the Salicaceae (willow family), the increasing prevalence of characteristic eastern North American taxa, the existence of a high altitude gymnosperm component, and the proliferation of dry-adapted (xeric) species in the Fossil Basin ecosystem.

Gymnosperms and environment of deposition

The Ruby flora, unique among the Fossil Basin palaeofloras, contains a significant proportion of gymnosperm genera (*Abies*, *Picea*, *Pinus*, *Psuedotsuga*) characteristic of the modern high altitude Rocky Mountain Montane forest association (Barbour & Billings 2000) and its Eocene Thunder Mountain ancestor (Axelrod 1998). This is likely due to differing environments of deposition, as only the Ruby flora is found in lacustrine host rocks (Fig. 6). Lake basins are well-known to incorporate material from multiple environments within their watersheds, in addition to wind-borne material, a phenomenon also observed in the Florissant lake beds (MacGinitie 1953, Meyer 2003) and the lacustrine Beaverhead Basins deposits (Becker 1969) both of which contain a similar high altitude component.

Geologic evidence and detrital zircon age dates (Link et al. 2008, Stroup et al. 2008, Lielke 2010, Rothfuss 2010, Lielke 2012, Rothfuss et al. 2012) suggest the presence of an ancestral Ruby Range, and related high elevation ecosystems, throughout Palaeogene southwestern Montana. Terrestrial gastropod faunas from the Eocene Climbing Arrow Member also demonstrate the juxtaposition of tropical and temperate forms which suggests mixing of high elevation and low elevation taxa in a region of moderate to high relief (Roth 1986). The absence of a high altitude component in the other Fossil Basin palaeofloras is therefore most likely an artifact of preservation.

Xeric vegetation & seasonal dryness

The Mormon Creek flora lacks a dry-adapted, or xeric, component which is consistent with

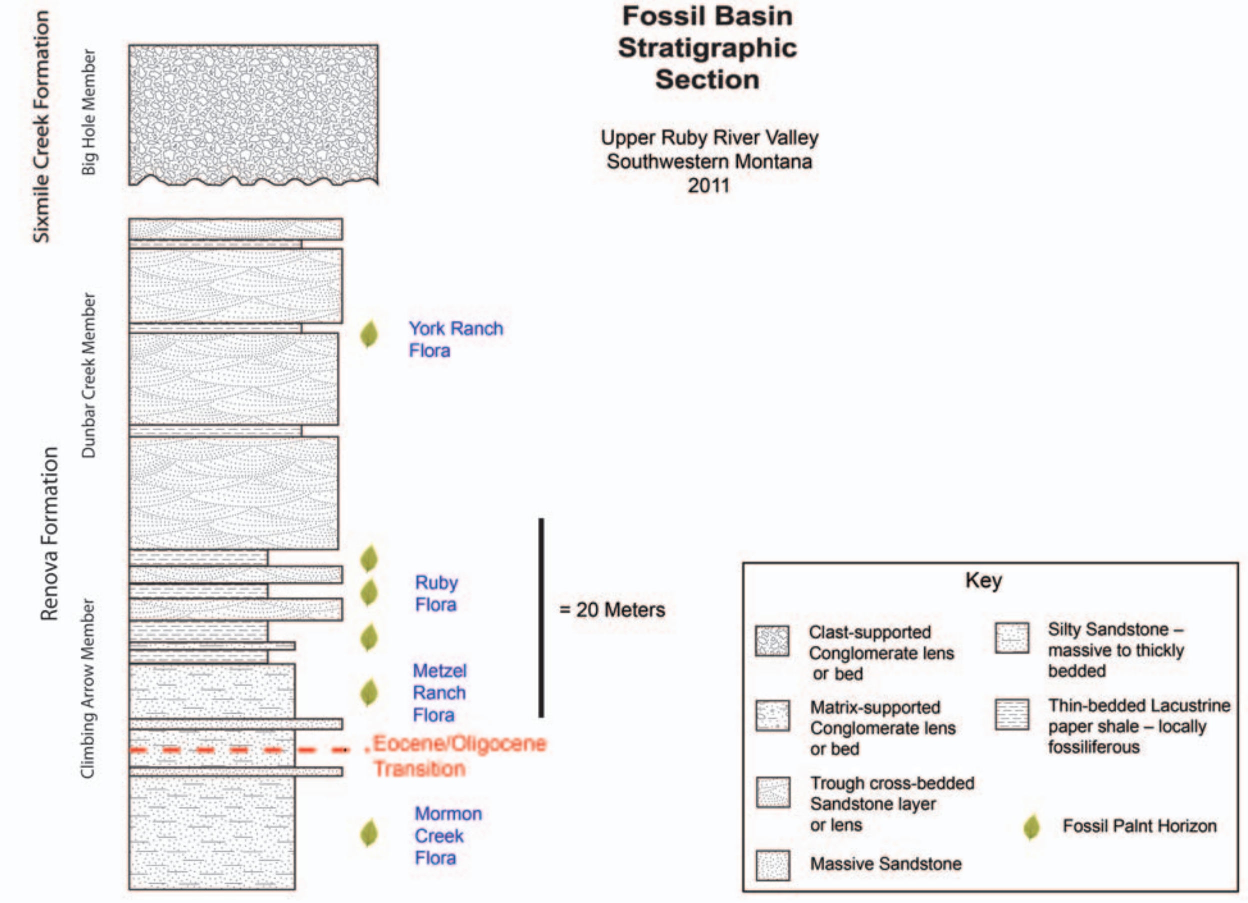

Fig. 6. Occurrence of fossil-bearing horizons within the stratigraphy of the Renova Formation. Note that the Fossil Basin paleofloras occur in three different sedimentary depositional environments (alluvial/fluvial overbank, open lake/near shore lacustrine & fluvial channel/overbank) and that these sediments appear to be conformable from late Eocene to early Oligocene time

its overall humid subtropical to warm temperate character (Becker 1960). However, coincident with the decline in three-driest months (3DRY) precipitation, a distinct xeric element entered the Metzel Ranch flora. This change in the Fossil Basin plant community is unlikely caused by preservation bias since both palaeofloras are found in an identical mudstone lithology interpreted as fluvial overbank, or basin flanking, distal alluvial fan deposits (Fig. 6). Similarity measures indicate that the Metzel Ranch flora has its greatest affinity with the Ruby flora despite differences in depositional environment (Tab. 5). The Metzel Ranch flora can probably be considered as representing a subgroup of the more inclusive Ruby flora.

The freshwater lake which accumulated the Ruby flora sampled multiple smaller plant communities or ecological niches, including an extensive xeric element, interpreted by Becker (1961) as occupying open woodland and barren hill slopes and benches between waterways. This xeric community includes fossil oaks (*Quercus*) of the nonlobed type, various pines, mountain mahogany (*Cercocarpus*), Oregon grape (*Mahonia*) and other xeric shrubs (Becker 1961). An almost identical arid community inhabited open dry woods and scrubland around late Eocene Lake Florissant in Colorado (Meyer 2003). This Palaeogene xeric community resembles the modern mountain mahogany – oak scrub vegetation found in the transition zone between montane coniferous forest and grassland/sagebrush scrub along the margins of the Rocky Mountains (Barbour & Billings 2000). Moreover, the presence of juniper (*Juniperus*) together with *Pinus* in both the Beaverhead Basins and Metzel Ranch floras suggests the Pinyon-Juniper woodlands of the semi-arid American southwest. It is hypothesized that both these modern ecotonal vegetation types evolved on the arid leeward side of high elevation, Eocene volcanic topography and expanded their range during more favorable Oligocene icehouse climatic

Table 5. Gower similarity coefficients determined from plant family presence/absence data for regional Paleogene paleofloras. A score of 1 indicates complete identity of plant families present in two fossil floras, a score of 0 indicates complete dissimilarity of plant families present between two paleofloras. Note that among the southwestern Montana paleofloras the oldest Mormon Creek and youngest York Ranch floras are outliers with greater similarity present between the early Oligocene floras

	Gower similarity – Gentry dataset																	
	Ruby	Mormon	Metzel	York	Christensen	Horse Prairie	Medicine Lodge	Florissant	Kissinger	Haynes	Bridge Creek	Creede	Thunder	Chalk Bluffs	Green River	Nut Beds	Republic	Buffalo Canyon
Ruby	1																	
Mormon	0.39	1																
Metzel	0.677	0.325	1															
York	0.353	0.306	0.4	1														
Christensen	0.433	0.257	0.56	0.32	1													
Horse Prairie	0.556	0.357	0.529	0.394	0.483	1												
Medicine Lodge	0.5	0.341	0.515	0.375	0.464	0.543	1											
Florissant	0.4	0.34	0.375	0.277	0.326	0.458	0.36	1										
Kissinger	0.238	0.359	0.263	0.355	0.3	0.405	0.282	0.375	1									
Haynes	0.364	0.314	0.414	0.4	0.524	0.452	0.536	0.372	0.281	1								
Bridge Creek	0.419	0.265	0.39	0.417	0.297	0.525	0.372	0.415	0.326	0.351	1							
Creede	0.424	0.333	0.433	0.276	0.478	0.306	0.5	0.298	0.194	0.5	0.333	1						
Thunder	0.344	0.189	0.345	0.269	0.364	0.387	0.414	0.239	0.182	0.455	0.333	0.417	1					
Chalk Bluffs	0.435	0.288	0.409	0.366	0.233	0.435	0.362	0.429	0.348	0.279	0.392	0.239	0.205	1				
Green River	0.333	0.356	0.302	0.316	0.306	0.5	0.349	0.542	0.474	0.324	0.383	0.214	0.175	0.429	1			
Nut Beds	0.208	0.229	0.227	0.297	0.184	0.261	0.217	0.263	0.286	0.175	0.4	0.14	0.154	0.36	0.265	1		
Republic	0.333	0.245	0.302	0.429	0.27	0.429	0.349	0.396	0.366	0.324	0.585	0.275	0.27	0.4	0.362	0.442	1	
Buffalo Canyon	0.375	0.184	0.429	0.308	0.55	0.375	0.448	0.349	0.333	0.571	0.361	0.522	0.476	0.286	0.297	0.179	0.333	1

conditions, probably in tandem with ancestral high altitude coniferous vegetation.

New palaeoclimate estimates suggest a seasonal, Oligocene summer dry climate with little summer precipitation and high temperatures consistent with the pronounced xeric vegetative element and the presence of land tortoises and gypsum (Dorr & Wheeler 1964, Monroe 1976). Terrestrial gastropod faunas also suggest an Oligocene environment drier than that of the Eocene with moderate seasonal variation in temperature and precipitation and sparse scrub, savannah, or open woodland vegetation (Roth 1986). Changes in sedimentary depositional environments and the composition of land snail faunas in the contemporaneous White River Formation of Wyoming indicate a similar shift from a humid subtropical late Eocene climate to a warm temperate climate with a pronounced dry season, accompanied by only a minor decrease in temperature near the E/O boundary (Evanoff, Prothero & Lander 1992). In the Pacific Northwest, Myers (2003) also reports a small (3–4°C) decline in MAT, a moderate increase in seasonality and a pronounced decrease in dry month precipitation across the E/O boundary. On a more global scale, the Eocene/Oligocene transition has also been linked to significant aridification and cooling in continental Asia (Dupont-Nivet et al. 2007). Alternatively, estimates based on the stable isotope composition of fossil teeth indicate a large drop in MAT, a small increase in seasonality and no change in aridity across the E/O transition in the White River beds of the Great Plains (Zanazzi et al. 2007, 2009). The exact reason for this discrepancy is unknown but could be due to differences in research methodology, local microclimates, rapid climate change coupled with variable preservation of fossil material, or chronostratigraphic difficulties.

Horizontal and cross-cutting layers and stringers of pedogenic gypsum are common in certain horizons of the laminated shale and mudstone facies at Fossil Basin. Mud cracks have also been observed in the lacustrine laminated shales containing the Ruby flora (Monroe 1976). The formation of gypsum in soil profiles is promoted by the presence of ashy volcanic material, typical of the Climbing Arrow Formation, but the most important requirement is a climate in which evapo-transpiration exceeds precipitation (Chen 1997, Retallack 2001). Although the annual precipitation calculated for Fossil Basin is higher than is typical for modern sites precipitating pedogenic gypsum (Mack & James 1994, Retallack 2001), a combination of seasonal wetness, capable of mobilizing salts from volcanic parent material, followed by a pronounced dry season capable of precipitating gypsum could account for the observed deposits. A thick mantle of volcanic ash would also tend to place the water table at greater depths promoting soil drying (Leopold & MacGinitie 1972). The York Ranch flora lacks a xeric element, but this is likely due to the riparian nature of the vegetation preserved in this fluvial environment.

East Asian endemics

Several taxa such as *Metasequoia*, *Ginkgo*, *Craigia*, and *Cercidiphyllum*, now restricted to East Asian localities, had an early Cenozoic circumpolar distribution in temperate latitudes (Graham 1998, 2011). These taxa gradually became extinct across the North American continent with only a few surviving into the late Neogene (Graham 1998, 2011). Except for *Cercidiphyllum*, East Asian endemics are uncommon in the Mormon Creek flora (Becker 1960). With the advent of more temperate conditions, East Asian temperate species became more common in the Metzel Ranch and Ruby floras with a maximum of 12 Genera present in the Ruby flora including *Gingko*, *Metasequoia*, *Cercidiphyllum*, *Ailanthus*, *Eucommia*, and *Glyptostrobus* (Becker 1972, 1964, 1961).

However, by the time of deposition of the York Ranch flora most representative East Asian endemics had disappeared, with only *Cercidiphyllum* and possibly *Metasequoia* being in evidence (Becker 1973). This may be due partially to the more restricted fluvial depositional environment of the Dunbar Creek Member which houses the York Ranch flora. However, many of these taxa are present in the Metzel Ranch flora which contains a comparable number of species and which was preserved in a similar, though not identical, sedimentary depositional environment. Moreover, the interpreted habitat of many of these missing taxa doesn't preclude their presence in a riparian environment (Myers 2003). Moreover, *Ailanthus* and *Eucommia* both possess wind distributed samaras which are capable of being widely distributed into a variety of different depositional environments.

The disappearance of so many East Asian endemics is unlikely to be solely a taphonomic artifact and therefore probably reflects local extinction of most of these lineages. Pronounced early Oligocene seasonal dryness would have been detrimental to wet-adapted taxa such as *Metasequoia* – a species reinterpreted by Retallack, Bestland & Fremd (1996) as a wetland inhabitant similar to living bald cypress (*Taxodium distichum*). Although somewhat colder and wetter, the climate indicated by the York Ranch flora was not much different than early Oligocene climate; however, one important threshold was crossed in the later Oligocene with cold month mean temperature (CMMT) dropping below 0°C (Fig. 4). This suggests prolonged, rather than episodic, winter freezing. This combination of increased summer dryness and winter cold, exacerbated by competition from pre-adapted species which had evolved in upland and orogenic rain shadow environments, likely caused the demise of the circumpolar, Palaeogene deciduous forest community in the northern Rocky Mountains. The disjunct modern deciduous forests of eastern North America and East Asia owe their existence to the formation of hostile intermontane climates favorable to the expansion of species previously confined to cold and dry upland habitats (i.e. high altitude montane coniferous forest and arid scrub/woodland rain shadow vegetation). The elimination of diverse hardwoods under a colder and drier continental climate was recognized by Leopold and MacGinitie (1972) as the final phase in the modernization of the Rocky Mountain flora.

Dominant Plant Families

The Fossil Basin palaeofloras preserve a suggestive sequence of changes in dominant plant families as indicated by the number of species present (grouped according to family). Table 6 lists every plant family represented by more than one species in order of decreasing number of species. The Mormon Creek flora has a rather wide diversity of plant families with no family represented by more than four species. The Mormon Creek flora is characterized by the prominence of the Fabaceae-Lauraceae association, a reflection of the subtropical component it uniquely contains. The three younger palaeofloras, despite their occurrence in different environments of deposition, are all dominated by the Salicaceae-Rosaceae-Ulmaceae association although the lacustrine Ruby flora also contains nine species of Pinaceae owing to the high elevation component it preserves. Although only represented by seven species combined, the Salicaceae-Rosaceae-Ulmaceae association is also an important secondary component of the Mormon Creek flora. It is hypothesized that this association rose to prominence following the elimination of the subtropical element in the Mormon Creek flora owing to its superior ability to withstand seasonal drought. Rosaceae is a common element in arid ecosystems while Salicaceae and Ulmaceae often inhabit riparian areas in modern dry climates.

The Betulaceae and Fagaceaee, previously not represented by more than one species, became an important secondary element in the Ruby flora. The appearance of the Juglandaceae in the York Ranch flora signaled the appearance of a distinctly eastern North American element, the Betulaceae-Fagaceae-Juglandaceae association, as can be seen by comparison with the composition of the York Ranch flora's nearest living analogs, all from eastern North America. The familial composition of the York Ranch flora gives it a distinctly modern riparian aspect (Barbour & Billings 2000) an interpretation strengthened by the presence of members of the Aceraceae, Cornaceae and Vitaceae. The modern aspect of the York Ranch flora is further enhanced by the elimination of most East Asian endemic species along with the extinct late Eocene lineages typified by the Florissant genus *Fagopsis*. This genus represents one of the most common fossils found at the Florissant locality (MacGinitie 1953); however, although present in the Ruby flora, *Fagopsis* leaves and fruits are uncommon. This suggests that, by the Oligocene, the southern Rocky Mountains element in Montana was either on the fringes of its environmental tolerances, subject to high competitive pressure from other riparian species, especially members of the Salicaceae, or both.

At Florissant, willows are rare and only one species of poplar is present (*P. crassi*) – although it is a common fossil – Meyer (2003)) suggesting habitat competition with Eocene riparian taxa like *Fagopsis* and *Cedrelospermum*, and possibly differing environmental tolerances. In southwestern Montana, the Salicaceae are by far the most dominant family by York Ranch time (15 species – although

Table 6. Number of species present for Fossil Basin paleofloras and their five nearest living analogs (NLA). Every plant family containing more than one species is represented. Dominant taxa for modern forest transect data are from Miller & Phillips (2002). Yellow, blue, green and red fields highlight plant family associations important for interpreting the evolution of Fossil Basin vegetation and its gradual convergence on modern forest associations

Mormon Creek Flora	Chiba (Japan)	Quinceoc (Mexico)	Valleyvi (Missouri)	Suderhac (Germany)	Avalanch (India)
Fabaceae (4)	Fagaceae (7)	Lauraceae (5)	Fagaceae (7)	Betulaceae (3)	Lauraceae (13)
Lauraceae (3)	Ericaceae (4)	Fabaceae (3)	Juglandaceae (3)	Fagaceae (2)	Rubiaceae (9)
Myricaceae (3)	Lauraceae (4)	Fagaceae (3)	Ulmaceae (2)	Rosaceae (2)	Myrtaceae (6)
Salicaceae (3)	Anacardiaceae (3)	Araceae (2)		Salicaceae (2)	Aquifoliaceae (5)
Celastraceae (3)	Theaceae (3)	Betulaceae (2)			Symplocaceae (4)
Sapindaceae (3)	Aquifoliaceae (2)	Celastraceae (2)			Piperaceae (3)
Ulmaceae (2)	Araliaceae (2)	Meliaceae (2)			Pittosporaceae (3)
Proteaceae (2)	Oleaceae (2)	Rutaceae (2)			Daphniphyllaceae (2)
Berberidaceae (2)					Theaceae (2)
Rosaceae (2)					
Aquifoliaceae (2)					
Rhamnaceae (3)					
Araliaceae (2)					
Oleaceae (2)					
# Species 54	47	47	23	15	69

Metzel Ranch Flora	Cuivre (Missouri)	Bankamp (Ohio)	Tysongla (Missouri)	Valleyvi (Missouri)	Huestomf (Ohio)
Salicaceae (9)	Juglandaceae (5)	Betulaceae (3)	Fagaceae (7)	Fagaceae (7)	Fagaceae (4)
Rosaceae (5)	Fagaceae (4)	Fagaceae (3)	Juglandaceae (5)	Juglandaceae (3)	Juglandaceae (3)
Ulmaceae (4)	Ulmaceae (4)	Rosaceae (3)	Rosaceae (4)	Ulmaceae (2)	Oleaceae (3)
Myricaceae (3)	Aceraceae (2)	Aceraceae (2)	Ulmaceae (2)		Fabaceae (2)
Rhamnaceae (3)	Fabaceae (2)	Juglandaceae (2)	Vitaceae (2)		Ulmaceae (2)
Fabaceae (3)	Oleaceae (2)	Ulmaceae (2)			Vitaceae (2)
Aceraceae (3)	Rosaceae (2)	Vitaceae (2)			
Sapindaceae (2)					
Alangiaceae (2)					
Anacardiaceae (2)					
Cupressaceae (2)					
# Species 59	29	23	26	23	24

Ruby Flora	Cuivre (Missouri)	Bankamp (Ohio)	Tysonwood (Missouri)	Bablersp (Missouri)	Allacher (Germany)
Rosaceae (10)	Juglandaceae (5)	Betulaceae (3)	Juglandaceae (5)	Juglandaceae (4)	Rosaceae (6)
Pinaceae (9)	Fagaceae (4)	Fagaceae (3)	Fagaceae (4)	Fagaceae (3)	Betulaceae (3)
Ulmaceae (6)	Ulmaceae (4)	Rosaceae (3)	Ulmaceae (3)	Ulmaceae (3)	Aceraceae (2)
Salicaceae (6)	Aceraceae (2)	Aceraceae (2)	Oleaceae (2)	Vitaceae (3)	Fagaceae (3)
Betulaceae (5)	Fabaceae (2)	Juglandaceae (2)	Vitaceae (2)	Aceraceae (2)	Pinaceae (2)
Fagaceae (5)	Oleaceae (2)	Ulmaceae (2)			
Sapindaceae (4)	Rosaceae (2)	Vitaceae (2)			
Aceraceae (4)					
Saxifragaceae (3)					
Myricaceae (3)					
Berberidaceae (3)					
Taxodiaceae (2)					
Anacardiaceae (2)					
# Species 82	29	23	23	23	21

York Ranch Flora	Bankamp (Ohio)	Potomac (Virginia)	Tysonwood (Missouri)	Cuivre (Missouri)	Rockcree (Missouri)
Salicaceae (15)	Betulaceae (3)	Aceraceae (3)	Juglandaceae (5)	Juglandaceae (5)	Betulaceae (2)
Rosaceae (7)	Fagaceae (3)	Betulaceae (2)	Fagaceae (4)	Fagaceae (4)	Fagaceae (2)
Ulmaceae (6)	Rosaceae (3)	Cornaceae (2)	Ulmaceae (3)	Ulmaceae (4)	
Betulaceae (5)	Aceraceae (2)	Fagaceae (2)	Oleaceae (2)	Aceraceae (2)	
Juglandaceae (3)	Juglandaceae (2)	Juglandaceae (2)	Vitaceae (2)	Fabaceae (2)	
Fagaceae (2)	Ulmaceae (2)	Magnoliaceae (2)		Oleaceae (2)	
Anacardiaceae (2)	Vitaceae (2)	Oleaceae (2)		Rosaceae (2)	
Lauraceae (2)		Ulmaceae (2)			
Vitaceae (2)					
# Species 58	23	25	23	29	17

Manchester et al. (2006) reassign three of these species to the extinct genus *Psuedosalix*) and the characteristic late Eocene element, so prominent at Florissant, is absent. In Colorado, a similar change occurred in the fossil floras which succeeded the Florissant – the Antero and Creede floras (Barton 2009, Axelrod 1987, Graham 1998, Meyer 2003). It is hypothesized that the Salicaceae enjoyed a climate-induced competitive advantage over riparian Florissant and East Asian Eocene holdovers; although the exact proportion of climate change versus habitat competition in driving these changes is difficult to distinguish from fossil data.

BEAVERHEAD BASINS PALAEOFLORAS

Palaeoclimate reconstructions and analysis of the taxonomic composition of the Beaverhead Basin palaeofloras largely support the previous interpretation of the Fossil Basin palaeofloras. However, before meaningful comparisons can be made, differences in the tectonic setting of the two locations need to be addressed as this has important implications for palaeoclimatic reconstruction. Published data (Janecke 2007, Link et al. 2008) and new field work (Lielke 2012, Rothfuss et al. 2012) suggest that the two areas differed in the presence of active Palaeogene normal faulting in the area of the Beaverhead Basins and its absence in the Fossil Basin area. The Beaverhead Basins lake beds (Medicine Lodge Formation) were deposited in the hanging wall of a Palaeogene low-angle normal fault proximal to the highlands of the coupled, uplifted footwall. This suggests the likelihood of lower elevation vegetation in the Beaverhead Basins. In order to test this possibility, two techniques for estimating palaeoelevation were employed. Palaeoelevations were calculated using the new estimates for MAT from this study and published lapse rates, and a new equation for enthalpy was calculated from the CLAMP-173 dataset and also used to estimate palaeoaltitude for each area.

PALAEOELEVATION ESTIMATES

Palaeobotanical remains have frequently been used in the past to estimate palaeoelevation (Gregory & McIntosh 1996, Meyer 2001). The two most common techniques involve either determining the elevation range of the nearest modern analogs of fossil taxa, or estimating elevation from palaeotemperature differences between coastal and inland localities. Mean annual temperature (MAT) can be reliably estimated from the morphology of fossil leaves (Bailey & Sinott 1915, Wolfe 1979), which are empirically linked to climate through basic angiosperm plant physiology (Givnish 1979, 1980). Once MAT's are determined for an inland site of interest and a contemporary coastal site at approximately the same latitude, palaeoelevation can be determined by assuming a terrestrial lapse rate (the rate of change of temperature with elevation).

However, terrestrial lapse rates vary widely on the modern Earth and would have behaved differently under ancient climate regimes, introducing considerable error into estimates of palaeoelevation (Forest et al. 1995, Wolfe 1995). One way to avoid this problem is to base elevation estimates on a fundamental parameter of atmospheric physics which would not vary over time and which would be conservative between coast and inland sites at the same latitude. One such physical parameter is moist static energy (h) which is a function of enthalpy (H) and elevation following the relation $H_c + gZ_c = h = H_i + gZ_i$ where Z_c = elevation of the coastal site, Z_i = elevation of the inland site, H_c = enthalpy at the coast, H_i = enthalpy of the inland site and g is the gravitational constant. If enthalpy can be reliably estimated, then elevation can be determined according to the ratio $Z_i = (H_c - H_i)/g$ (Forest et al. 1995). Enthalpy, as a function of temperature and humidity, has an empirically determinable relationship to leaf morphology. This relationship can be exploited to estimate the enthalpy of palaeofloral sites (Forest et al. 1995).

For this study, new multivariable equations were calculated for mean annual temperature (MAT) and enthalpy using the CLAMP-173 database. Cannonical correspondence analysis (CCA) was used as a tool to examine which leaf characters most closely correlate with MAT and enthalpy (Wolfe 1995). Multiple linear regression was used to calculate multivariable equations relating MAT and enthalpy to the selected leaf characteristics. The equations determined for MAT and enthalpy are statistically significant ($r^2 = .89$ for MAT and .85 for enthalpy) with standard errors of ±1°C and ±5 kJ/kg respectively. However, the possible bias associated with leaf size in the CLAMP dataset (Peppe et al. 2010) could lead to larger errors than calculated here.

Enthalpy and MAT were calculated for the palaeofloras of southwestern Montana and, by comparison with published MAT and enthalpy for Eocene and Oligocene coastal floras, palaeoelevations for southwestern Montana were calculated. In order to test whether estimates from these new equations are compatible to those previously determined for western North America, MAT and enthalpy were calculated for the Pitch-Pinnacle palaeoflora in Colorado (from raw physiognomy scores reported in Gregory and McIntosh (1996). New estimates for Pitch-Pinnacle are virtually identical for enthalpy (304.7 vs. 303.3 kJ/kg) and MAT (12.5 vs. 12.7°C) suggesting that coastal MAT and enthalpy reported by Gregory and McIntosh (1996) can be used to reliably estimate palaeoelevation for southwestern Montana.

Results from palaeoelevation estimates are summarized in Figure 7. Results from both methods lead to a relative difference in elevation of 0.7 to 1.0 km between the Fossil Basin area and the Beaverhead Basins area. Assuming that the Ruby, Metzel and Beaverhead Basin's floras are early Oligocene in age, the elevation during the early Oligocene would be ~2.5 km for the Fossil Basin area and ~1.5 km for the Beaverhead Basins area using the enthalpy method, or ~1.0 km and ~0.3 km respectively using MAT and a terrestrial lapse rate of 3°C/km. If any of these palaeofloras correlate to the late Eocene warm period which occurred just prior to the E/O boundary, then elevation estimates would be considerably higher (3 to 4 km for Fossil Basin) although the relative elevation difference is about the same (0.7–1.0 km). These estimates are similar to palaeoelevation estimates from other Palaeogene palaeofloral sites (Gregory 1994, Wolfe et al. 1998, Meyer 2001). Recent palaeoelevation estimates from stable isotope analysis also support the existence of high altitude Palaeogene topography in western North America, including the Sage Creek Basin in southwestern Montana (Mix et al. 2011).

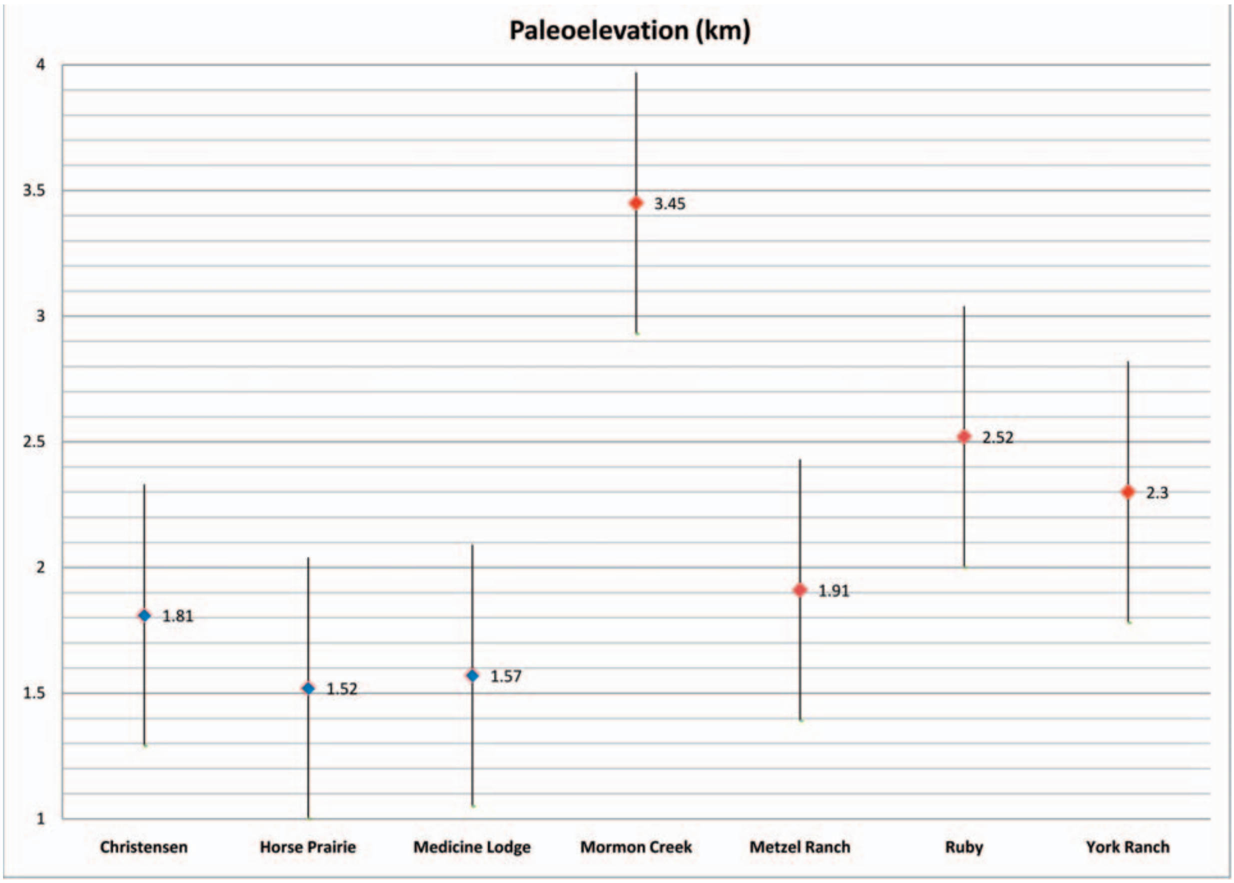

Fig. 7. Paleoelevation estimates (in kilometers) derived from enthalpy for the Beaverhead Basins (blue) and Fossil Basin (red) paleofloral sites. Mormon Creek estimate is an outlier probably due to the fact that its age is poorly constrained relative to the other paleofloras. The Beaverhead Basins paleofloras are closest in age to the Ruby flora suggesting an approximate paleoelevation difference of 1.0 ± 0.5 km in the early Oligocene

PALAEOCLIMATE ESTIMATES

The Beaverhead Basins palaeofloras are similar in age to the Metzel Ranch and Ruby palaeofloras and their palaeoclimate estimates are broadly similar. The most significant differences can probably be attributed to the lower elevation of the Beaverhead Basins area. Palaeotemperature estimates show somewhat higher MAT (~14–15°C) and less seasonality of temperature due to both higher cold month mean temperature (CMMT) and lower warm month mean temperature (WMMT) (Fig. 8). A difference in mean annual temperature of ~2°C is expected for an elevation difference of ~0.7 to 1.0 km assuming a terrestrial lapse rate of 3.0°C/km (Wolfe 1992) although it should be noted that local lapse rates can be highly variable.

Palaeoprecipitation estimates show a dramatic increase in growing season precipitation (GSP) and three wettest months (3WET) precipitation and a consistently low three driest months (3DRY) precipitation of 7–9 cm (Fig. 9). These estimates are consistent with the trend seen between the Metzel Ranch and Ruby floras suggesting that the Beaverhead Basins palaeofloras are registering the same climate shifts. Precipitation variations are likely due to waxing and waning glaciation in the southern hemisphere (Zachos et al. 1992) and possibly Greenland (Eldrett et al. 2007). Similar cyclical changes in Palaeogene precipitation, interpreted as alternating glacial/interglacial cycles, are also recorded by calcic palaeosols in the Sage Creek Basin of southwestern Montana (Sheldon 2009).

NEAREST LIVING ANALOGS

Nearest living analogs (NLA) for the Beaverhead Basins palaeofloras are similar to those determined for the Metzel Ranch and Ruby floras (Tab. 3) with all NLA from central and eastern North America and Europe. Euclidean distance calculations also reveal close affinities with East Asian temperate localities in the CLAMP-173 database. Gentry NLA sites mostly fall under the warm temperate dry and warm temperate moist Holdridge zones with lesser representation of the cool temperate moist and boreal wet zones. The conifer dominated European NLA sites, which represent

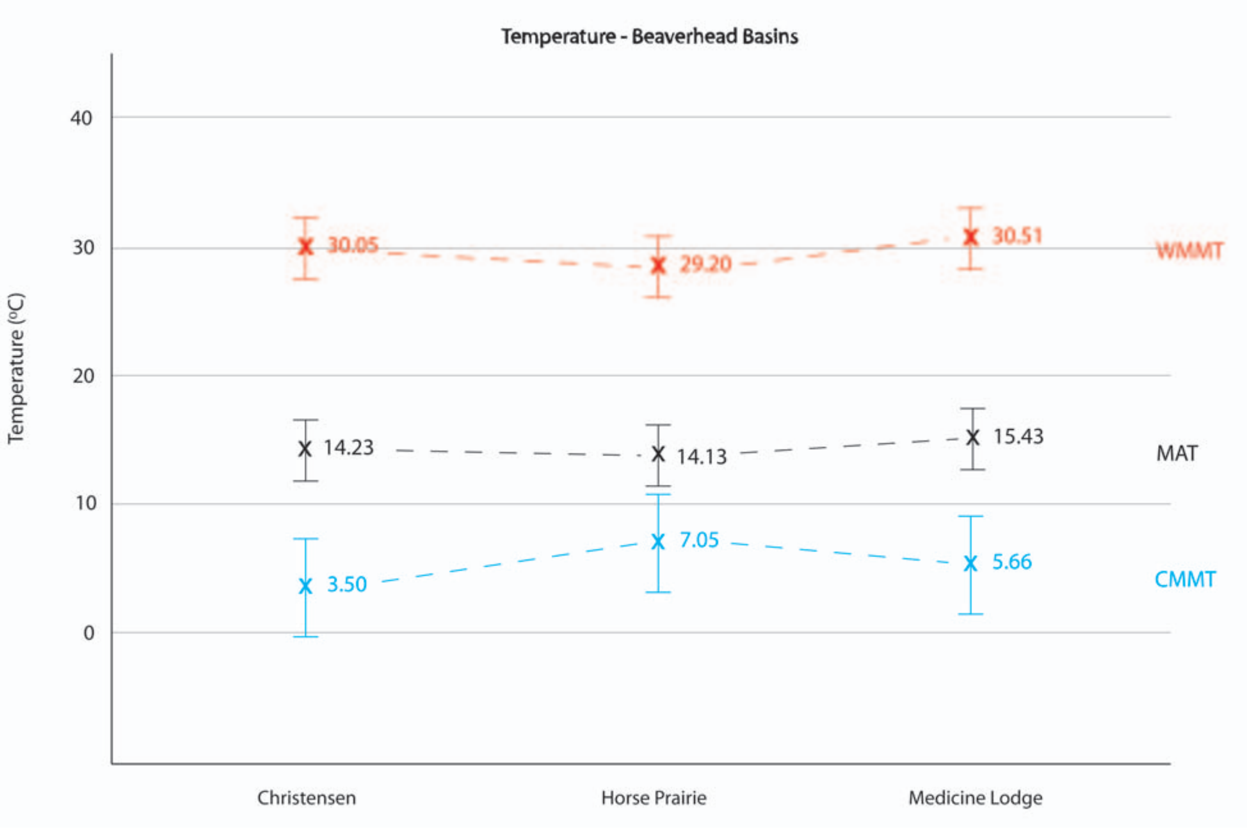

Fig. 8. New paleotemperature estimates for the Beaverhead Basins paleofloras. WMMT = warm month mean temperature, MAT = mean annual temperature, and CMMT = cold month mean temperature. Standard errors are: ±2.5°C for WMMT, ±2.4°C for MAT and ±3.6°C for CMMT

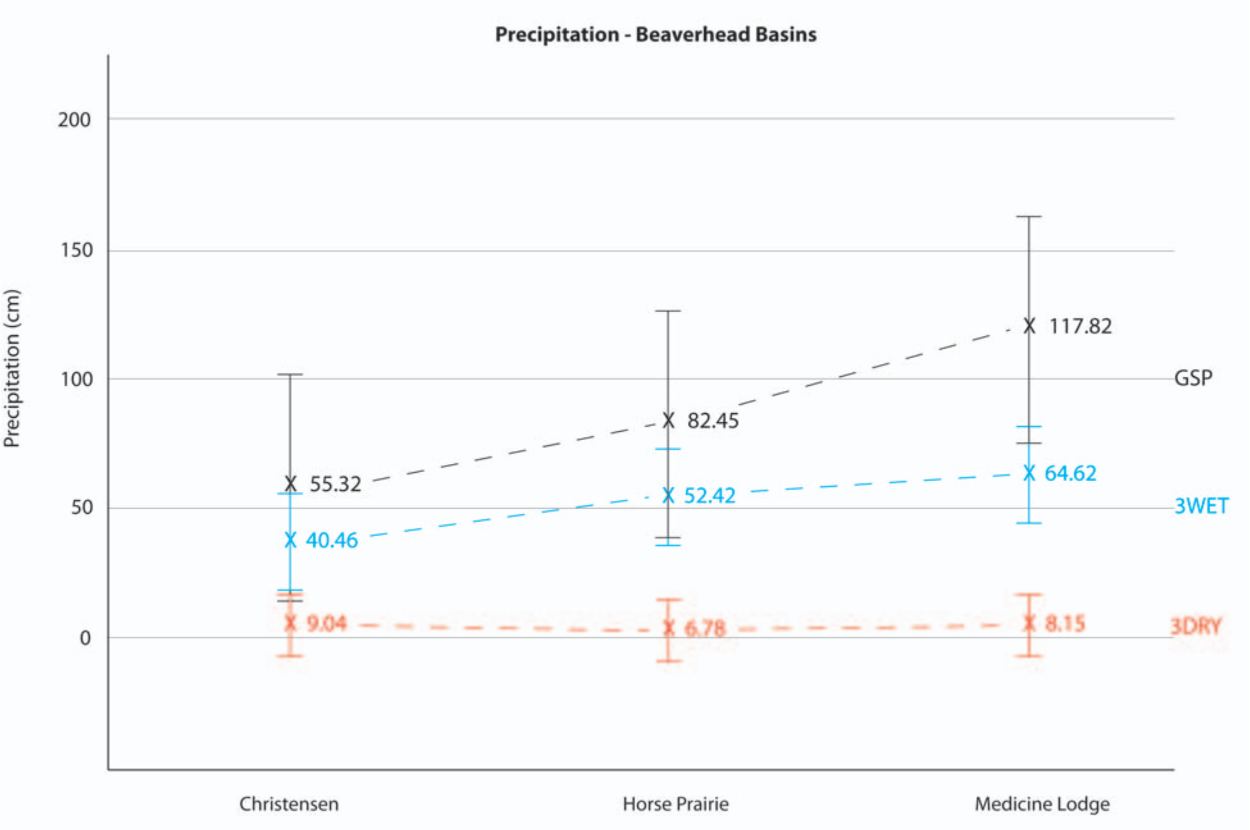

Fig. 9. New paleoprecipitation estimates for the Beaverhead Basins paleofloras. GSP = growing season precipitation, 3WET = precipitation for the three wettest months and 3DRY = precipitation for the three driest months. Standard errors are: ±42.5 cm for GSP, ±17.5 cm for 3WET and ±11.6 cm for 3DRY

most of the cool temperate moist and boreal wet zones, are interpreted as proxies for the Rocky Mountain coniferous forest association. The proximity of the Palaeogene lake deposits to the uplifted footwall of the basin bounding Muddy Creek/Grasshopper normal fault system (Dunlap 1982, Matoush 2002, Janecke 2007) probably accounts for the high elevation, conifer-rich element present in all the Beaverhead Basins palaeofloras. The taxa present are largely identical to the high altitude community preserved in the Ruby flora suggesting a regional, high altitude forest association directly ancestral to the modern Rocky Mountain coniferous forest association.

A xeric community containing most of the same species, or very closely related forms, as the Metzel Ranch and Ruby floras demonstrates the existence of a regional dry-adapted plant community in the Palaeogene northern Rocky Mountains. Similar species of *Cercocarpus*, *Mahonia*, *Pinus*, and *Quercus* are also known from the Florissant locality (MacGinitie 1953). Moreover, *Ephedra* palynomorphs have also been reported from the Medicine Lodge flora (Leopold & MacGinitie 1972). *Ephedra*, a genus which thrives today in dry habitats, is also known from Florissant, further strengthening the case for a regional xeric community bracketing the Eocene/Oligocene (E/O) boundary. These observations suggest that a highly seasonal, summer dry climate was present throughout the northern Rocky Mountains and likely stretched further south along the cordillera. Moreover, the southwestern Montana palaeofloras appear to contain plant associations ancestral to both the mountain mahogany and juniper scrub associations of the modern Rocky Mountains (Barbour & Billings 2000).

Another trend of interest observed in the Beaverhead Basins palaeofloras, which also has a parallel in the Fossil Basin locality, is a temporary increase in species of East Asian affinity near the E/O boundary. The number of East Asian species increased in the transitional floras of the Fossil Basin locality before practically disappearing by York Ranch time. Similarly, in the Beaverhead Basins area, the number of species of East Asian affinity increased from 16 to 25 to 32 from Christensen

Ranch to Horse Prairie to Medicine Lodge time (Becker 1960). This suggests that during the transitional period straddling the E/O boundary, temperate East Asian taxa temporarily became a more prominent component of northern Rocky Mountains vegetation before gradually losing out to North American temperate forms directly ancestral to modern vegetation.

COMPARISON WITH OTHER PALAEOGENE PALAEOFLORAS

In order to place the Montana palaeofloras in the larger context of Palaeogene vegetation, Gower similarity coefficients were calculated for the plant family abundances of the Montana palaeofloras and several representative western North American Palaeogene fossil localities (Tab. 5). The top ten nearest living analog (NLA) sites for these regional palaeofloras were also calculated from the Gentry dataset and are summarized as Holdridge Life Zones in Table 7. The most obvious trend in this regional data is the elimination of tropical and subtropical communities across the E/O boundary. This same phenomenon was previously noted in the transition from the Mormon Creek to the Metzel Ranch palaeoflora.

The Thunder Mountain flora in Idaho, an Eocene high elevation flora, has NLA representative of the Boreal Wet and Cool Temperate Moist Holdridge zones suggesting that NLA representative of these zones serve as a proxy for high elevation Rocky Mountain coniferous forest. These Holdridge zones become common in Oligocene and Miocene localities, including the Montana sites, suggesting the expansion of this forest type from isolated, mostly volcanic Eocene highlands, such as the Thunder Mountain caldera, to a dominant Oligocene forest type on a regional scale (Wolfe 1987).

There is also a north/south gradient apparent in the Eocene NLA sites. Tropical Holdridge zones are confined to the most southerly sites, the Green River and Florissant localities, dying out northward with only one tropical NLA in the Kissinger locality of northern Wyoming (although Kissinger reconstructions based on lower taxonomic levels are more tropical in character (MacGinitie 1974)) and none in the Republic flora – even though the Republic and Kissinger sites are both older than the Florissant locality. By late Eocene (Mormon Creek flora) time, the northern Rocky Mountains were mesic and temperate, the central

Table 7. Holdridge life zones based on nearest living analogs (NLA) from the Gentry database for eleven representative western North American paleofloral localities. Blue fields represent Eocene localities, red fields Oligocene localities and green Miocene. Note the progressive elimination of tropical and subtropical Holdridge zones across the Eocene/Oligocene transition. Cool temperate and boreal wet Holdridge zones occur in paleofloras with a pronounced high altitude component. Eocene paleofloras demonstrate that a considerable diversity of plant communities once coexisted probably due to elevational zonation, extensive micro-niches (e.g. arid communities in the rainshadow of volcanoes) and a wider range of environmental tolerances within individual plant families

Localities Climate	Nutbeds	Republic	Chalk Bluffs	Green River	Kissinger	Thunder Mtn.	Florissant	Bridge Creek	Haynes	Creede	Buffalo Canyon
Tropical Premontane Dry				1			1				
Tropical Moist				1			1				
Tropical Montane Moist				1							
Tropical Premontane Wet				1	1		1				
Tropical Wet				1			1				
Subtropical Moist				2			1				
Subtropical Montane Moist	2		1				1				
Subtropical Wet	1		2	1			1				
Subtropical Montane Wet				1							
Subtropical Rain Forest				1							
Warm Temperate Wet											
Warm Temperate Moist	4	5	3		3	1	1	4	1	3	3
Warm Temperate Montane Moist					1						
Warm Temperate Dry	3	5	4		4	1	2	5	4	3	3
Cool Temperate Rain forest						2					
Cool Temperate Moist					1	3		1	3	2	3
Boreal Wet						3			2	2	1

Rocky Mountains seasonally dry and temperate, and the southern Rocky Mountains were subtropical and seasonally dry (Leopold & MacGinitie 1972, Wing 1987, Wolfe 1987, Graham 1998, 2011).

Across the Eocene/Oligocene transition and through the Oligocene period, warm temperate dry forest expanded and seasonal dry conditions became strongly established in the northern Rocky Mountains. The Gower similarity measure shows that the Montana palaeofloras have their greatest affinity with regional Oligocene and Miocene localities, as expected, but also have close affinities with the more northerly Eocene sites such as the Republic flora. This suggests a degree of continuity of Palaeocene vegetation in the northern Rocky Mountains region across the Eocene /Oligocene boundary.

CONCLUSIONS

The following conclusions are suggested by compositional and statistical analysis of the palaeofloras of southwestern Montana:

1) The late Eocene Mormon Creek flora predates the final Palaeogene greenhouse climatic deterioration and retains a distinct component of subtropical vegetation. The climate was warm and relatively wet without a distinct summer dry season, an interpretation also supported by terrestrial gastropod faunas.

2) The Metzel Ranch and Ruby floras, along with the Beaverhead Basins palaeofloras, are transitional assemblages which existed for a relatively short period of time in the immediate aftermath of the Eocene/Oligocene climatic deterioration. The most important changes which occurred during this time were the elimination of the remaining subtropical Eocene taxa and the development of a distinct xeric plant assemblage. These biotic changes correspond to a sharp decline in precipitation during the three driest months which, coupled with a continuation of high summer temperatures, signaled the initiation of a climate regime with a distinct dry season. Similar cooling and drying tends, and associated floral shifts, are recorded from other western North American localities.

3) Ancestral versions of the modern, high altitude Rocky Mountain Montane coniferous forest and the moderate elevation mountain mahogany/juniper scrub woodland expanded their range, from isolated volcanic highlands in the Eocene, to dominant components of Oligocene western North American vegetation.

4) During the Eocene/Oligocene transitional period, taxa with East Asian affinities temporarily became a more prominent element in the regional flora. East Asian taxa were eventually replaced by species ancestral to modern North American riparian and deciduous forest taxa.

5) Elevations were ~0.7 to 1.0 km lower in the Beaverhead Basins area relative to the Fossil Basin locality due to the former's location in the hanging wall of an Eocene normal fault system. Higher mean annual temperature and a less seasonal climate in the Beaverhead Basins area are attributable to deposition at a lower altitude.

6) During deposition of the Oligocene York Ranch flora, vegetation assumed a more modern North American aspect with the elimination of East Asian endemics and late Eocene holdovers, and a corresponding increase in taxa related to deciduous forms common to the forests of central and eastern North America.

7) Cyclical patterns of precipitation observed in the Montana palaeofloras are likely due to the growth and decline of Antarctic continental glaciation. By the early Oligocene, cold month mean temperatures dropped below 0°C for the first time, suggesting prolonged, rather than episodic, winter freezing events. Competition from species better adapted to icehouse climate was also an important factor in the regional extinction of Eocene greenhouse taxa.

8) Across the Eocene/Oligocene boundary, overall plant diversity declined due to the loss of tropical/subtropical communities and the elimination of specialist taxa within multiple plant families. Previously marginal communities, such as high elevation coniferous and xeric vegetation, greatly expanded their range in the cooler and drier ice house climate of the post-Eocene world.

9) During times of rapid climatic overturn, apparently disjoint associations of plants (e.g. temperate and subtropical/tropical taxa) can temporarily occur together as their extreme climatic tolerances converge and overlap. This is particularly true in areas of high relief, and associated altitude specific climate zones, like the Palaeogene Rocky Mountain region.

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APPENDIX

Appendix 1. Multiple Linear Regression statistics

MAT

SUMMARY OUTPUT	
Regression Statistics	
Multiple R	0.940040557
R Square	0.883676248
Adjusted R Square	0.878741301
Standard Error	2.370635788
Observations	173

ANOVA

	df	SS	MS	F	Significance F
Regression	7	7044.308981	1006.329854	179.0649906	1.1951E-73
Residual	165	927.2858162	5.619914038		
Total	172	7971.594798			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	12.84639352	2.364602183	5.432792719	1.95996E–07	8.177615163	17.51517188	8.177615163	17.51517188
No Teeth	0.157136162	0.026254259	5.985168444	1.30637E–08	0.105298557	0.208973768	0.105298557	0.208973768
Emarginate apex	0.08173152	0.020402505	4.005955107	9.32596E–05	0.041447884	0.122015157	0.041447884	0.122015157
Acute teeth	0.051010577	0.031427188	1.623135292	0.106469504	–0.011040695	0.113061849	–0.011040695	0.113061849
Regular teeth	–0.079724891	0.037767338	–2.110948121	0.036283782	–0.154294446	–0.005155337	–0.154294446	–0.005155337
L:W <1:1	–0.218890155	0.042156664	–5.19230255	6.04841E–07	–0.302126194	–0.135654115	–0.302126194	–0.135654115
Round base	–0.045054163	0.01944873	–2.31656067	0.02175723	–0.083454622	–0.006653704	–0.083454622	–0.006653704
Leptophyll 2	–0.161456758	0.030998668	–5.208506354	5.61203E–07	–0.222661941	–0.100251575	–0.222661941	–0.100251575

WMMT

SUMMARY OUTPUT	
Regression Statistics	
Multiple R	0.891571158
R Square	0.79489913
Adjusted R Square	0.782238582

Standard Error	2.49788549
Observations	173

ANOVA

	df	SS	MS	F	Significance F
Regression	10	3917.460121	391.74601	62.7855255	1.52222E–50
Residual	162	1010.787972	6.2394319		
Total	172	4928.248092			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	40.0886801	4.175906135	9.5999955	1.4767E–17	31.84245249	48.33490771	31.84245249	48.33490771
No Teeth	–0.121462848	0.045580908	–2.6647747	0.00848349	–0.211472184	–0.03145351	–0.211472184	–0.031453512
Round teeth	–0.192571649	0.035959805	–5.3551917	2.8866E–07	–0.263582042	–0.12156126	–0.263582042	–0.121561256
Compound teeth	–0.293783254	0.035651474	–8.2404237	5.5029E–14	–0.364184782	–0.22338173	–0.364184782	–0.223381726
Regular teeth	–0.034520618	0.040708587	–0.8479935	0.39769274	–0.114908506	0.045867269	–0.114908506	0.045867269
Leptophyll 2	–0.143214148	0.042247485	–3.3898858	0.00087828	–0.226640921	–0.05978737	–0.226640921	–0.059787375
Mesophyll 3	–0.172388662	0.075249553	–2.2908928	0.02325846	–0.32098514	–0.02379218	–0.32098514	–0.023792184
Nanophyll	0.191574601	0.035853631	5.3432413	3.0531E–07	0.120773872	0.26237533	0.120773872	0.26237533
Emarginate apex	0.035498788	0.024419902	1.4536827	0.14796882	–0.012723577	0.083721153	–0.012723577	0.083721153
Cordate base	0.132325495	0.038155578	3.4680511	0.00067158	0.056979074	0.207671917	0.056979074	0.207671917
L:W <1:1	–0.165334698	0.051472891	–3.2120733	0.0015898	–0.266979026	–0.06369037	–0.266979026	–0.06369037

CMMT

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.924062869
R Square	0.853892187
Adjusted R Square	0.846764976
Standard Error	3.605225323
Observations	173

ANOVA

	df	SS	MS	F	Significance F
Regression	8	12457.71159	1557.213949	119.8073492	1.97126E–64
Residual	164	2131.614539	12.99764963		
Total	172	14589.32613			

Appendix 1. Continued

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	–4.521630393	3.147257061	–1.436689252	0.152711263	–10.73599816	1.692737375	–10.73599816	1.692737375
No Teeth	0.213394471	0.044133548	4.835198635	3.04165E–06	0.126251256	0.300537686	0.126251256	0.300537686
Emarginate apex	0.159580804	0.030371973	5.254212636	4.56774E–07	0.099610295	0.219551314	0.099610295	0.219551314
Mesophyll 1	0.09261901	0.080081524	1.156559031	0.249134494	–0.065504725	0.250742744	–0.065504725	0.250742744
Lobed	0.194546832	0.064679144	3.007875813	0.003045698	0.066835629	0.322258036	0.066835629	0.322258036
Leptophyll 1	–0.153091264	0.062180887	–2.462030892	0.014849837	–0.275869572	–0.030312955	–0.275869572	–0.030312955
Mesophyll 2	0.274091434	0.10886742	2.517662618	0.012772677	0.059128953	0.489053915	0.059128953	0.489053915
Close teeth	–0.062505576	0.04239074	–1.474510167	0.142261339	–0.146207556	0.021196403	–0.146207556	0.021196403
L:W <1:1	–0.418943835	0.080602569	–5.197648638	5.93594E–07	–0.578096392	–0.259791278	–0.578096392	–0.259791278

GROWSEA

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.928988236
R Square	0.863019143
Adjusted R Square	0.854563534
Standard Error	1.188066724
Observations	173

ANOVA

	df	SS	MS	F	Significance F
Regression	10	1440.645837	144.0645837	102.0647002	1.32825E–64
Residual	162	228.6634117	1.411502541		
Total	172	1669.309249			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	6.028548373	1.628917311	3.700954206	0.000293963	2.811899705	9.245197041	2.811899705	9.245197041
No Teeth	0.063960427	0.018436428	3.469241906	0.000668815	0.027553723	0.100367131	0.027553723	0.100367131
Emarginate apex	0.022482066	0.010347689	2.172665309	0.031258614	0.002048321	0.042915811	0.002048321	0.042915811
Mesophyll 1	0.081005068	0.018976375	4.268732451	3.33719E–05	0.043532121	0.118478015	0.043532121	0.118478015
Lobed	0.052190108	0.021579337	2.418522368	0.016691996	0.009577052	0.094803164	0.009577052	0.094803164
Close teeth	–0.036246931	0.01897052	–1.9106978	0.057809705	–0.073708317	0.001214454	–0.073708317	0.001214454
L:W <1:1	–0.173459069	0.028697223	–6.044454833	9.97388E–09	–0.230127928	–0.116790211	–0.230127928	–0.116790211
Cordate base	0.03277895	0.018779715	1.745444519	0.082803499	–0.004305648	0.069863548	–0.004305648	0.069863548
Round teeth	–0.02463646	0.014231834	–1.731081097	0.085341226	–0.052740287	0.003467368	–0.052740287	0.003467368

Compound teeth	–0.006449689	0.018517086	–0.348310158	0.728059481	–0.043015671	0.030116292	–0.043015671	0.030116292
Ovate	0.00532527	0.013284567	0.400861419	0.689050355	–0.020907974	0.031558514	–0.020907974	0.031558514

GSP

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.887291859
R Square	0.787286843
Adjusted R Square	0.771333356
Standard Error	42.454697
Observations	173

ANOVA

	df	SS	MS	F	Significance F
Regression	12	1067358.009	88946.50073	49.34888855	1.68805E–47
Residual	160	288384.2075	1802.401297		
Total	172	1355742.216			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	–13.47467435	35.01027214	–0.384877738	0.70083912	–82.61651416	55.66716545	–82.61651416	55.66716545
Attenuate apex	1.701160144	0.339259283	5.014336316	1.39957E–06	1.031156468	2.371163819	1.031156468	2.371163819
Nanophyll	–2.313779972	0.812453638	–2.8478917	0.004979044	–3.918295901	–0.709264044	–3.918295901	–0.709264044
Leptophyll 1	0.565626396	1.178350692	0.48001533	0.631872061	–1.761500181	2.892752973	–1.761500181	2.892752973
Leptophyll 2	–1.580961651	1.089634165	–1.4509105	0.148762504	–3.732881823	0.570958522	–3.732881823	0.570958522
Mesophyll 1	0.329753985	1.209738021	0.272582972	0.785525274	–2.059359476	2.718867445	–2.059359476	2.718867445
Mesophyll 2	0.429924577	1.290011862	0.333271801	0.739365447	–2.117721816	2.977570969	–2.117721816	2.977570969
Round teeth	–1.205723436	0.383287128	–3.145744663	0.001975733	–1.962677768	–0.448769104	–1.962677768	–0.448769104
Acute teeth	–1.132790484	0.33158232	–3.416317503	0.000804755	–1.787632913	–0.477948055	–1.787632913	–0.477948055
L:W <1:1	–0.82186401	0.775523285	–1.059754137	0.290853646	–2.353446127	0.709718108	–2.353446127	0.709718108
L:W 2–3:1	1.715080112	0.516974949	3.317530404	0.001124197	0.694105497	2.736054727	0.694105497	2.736054727
L:W 3–4:1	3.822030381	0.822665652	4.645909758	7.03006E–06	2.197346731	5.446714031	2.197346731	5.446714031
Elliptic	1.499882875	0.422727282	3.548109945	0.000509442	0.665038121	2.33472763	0.665038121	2.33472763

Appendix 1. Continued

MMGSP

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.884661393
R Square	0.78262578
Adjusted R Square	0.770623523
Standard Error	4.415153868
Observations	173

ANOVA

	df	SS	MS	F	Significance F
Regression	9	11439.98366	1271.109296	65.20654781	1.90426E–49
Residual	163	3177.454139	19.49358368		
Total	172	14617.4378			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	–11.12530707	2.764285232	–4.024659591	8.71829E–05	–16.58373265	–5.666881494	–16.58373265	–5.666881494
Attenuate apex	0.192655795	0.031816537	6.055209505	9.3492E–09	0.12983008	0.25548151	0.12983008	0.25548151
Mesophyll 3	0.128346567	0.126596083	1.013827322	0.31216769	–0.12163317	0.378326304	–0.12163317	0.378326304
Round teeth	–0.123478707	0.038826597	–3.180260854	0.001761543	–0.20014666	–0.046810754	–0.20014666	–0.046810754
L:W 2–3:1	0.161233433	0.053091094	3.036920521	0.002783744	0.056398454	0.266068413	0.056398454	0.266068413
L:W 3–4:1	0.422634743	0.083749456	5.046417748	1.19145E–06	0.257261008	0.588008479	0.257261008	0.588008479
Elliptic	0.228141947	0.042914538	5.316192533	3.4428E–07	0.143401845	0.312882049	0.143401845	0.312882049
Regular teeth	0.088840068	0.031803486	2.793406605	0.005840565	0.026040122	0.151640013	0.026040122	0.151640013
L:W <1:1	–0.128790231	0.080820862	–1.593527061	0.112979281	–0.288381093	0.03080063	–0.288381093	0.03080063
Nanophyll	–0.10971351	0.058131595	–1.887330113	0.060893502	–0.224501586	0.005074567	–0.224501586	0.005074567

3WET

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.886697789
R Square	0.78623297
Adjusted R Square	0.774429882
Standard Error	17.54538187
Observations	173

ANOVA

	df	SS	MS	F	Significance F
Regression	9	184554.1358	20506.01509	66.61248304	4.94676E–50
Residual	163	50177.98928	307.840425		
Total	172	234732.1251			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	–18.55676986	11.23028644	–1.652386158	0.100380827	–40.73236954	3.618829827	–40.73236954	3.618829827
Attenuate apex	0.896231649	0.129269016	6.933073948	9.13899E–11	0.640973872	1.151489427	0.640973872	1.151489427
Nanophyll	–0.806316932	0.231156529	–3.488185845	0.00062534	–1.262764297	–0.349869567	–1.262764297	–0.349869567
Mesophyll 2	0.476681893	0.406894626	1.171511892	0.243102688	–0.326782239	1.280146025	–0.326782239	1.280146025
Round teeth	–0.460363177	0.156910433	–2.933923312	0.003829938	–0.770202375	–0.150523979	–0.770202375	–0.150523979
Acute teeth	–0.113126182	0.132983917	–0.85067566	0.396197438	–0.375719494	0.149467131	–0.375719494	0.149467131
L:W <1:1	–0.630582966	0.309113152	–2.039974557	0.04296696	–1.240965396	–0.020200536	–1.240965396	–0.020200536
L:W 2–3:1	0.520491009	0.213349983	2.439611209	0.015775121	0.099204888	0.941777129	0.099204888	0.941777129
L:W 3–4:1	1.775115507	0.334076048	5.313507258	3.48632E–07	1.115440729	2.434790284	1.115440729	2.434790284
Elliptic	0.754415208	0.170742981	4.418425898	1.8065E–05	0.417261921	1.091568495	0.417261921	1.091568495

3DRY

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.878025357
R Square	0.770928528
Adjusted R Square	0.75975431
Standard Error	11.58148119
Observations	173

ANOVA

	df	SS	MS	F	Significance F
Regression	8	74031.265	9253.908124	68.99171981	1.50648E–48
Residual	164	21997.43588	134.1307066		
Total	172	96028.70087			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	–39.66447759	5.995264185	–6.615968266	4.98852E–10	–51.5023338	–27.82662139	–51.5023338	–27.82662139
Attenuate apex	0.511525341	0.084022176	6.08798016	7.83466E–09	0.345620652	0.67743003	0.345620652	0.67743003
Mesophyll 3	0.513202542	0.627744762	0.817533769	0.414809585	–0.726301173	1.752706256	–0.726301173	1.752706256
Mesophyll 2	–0.931349259	0.504351786	–1.846626273	0.066603506	–1.927209281	0.064510762	–1.927209281	0.064510762

Appendix 1. Continued

Round teeth	–0.22090884	0.086687809	–2.548326489	0.011742311	–0.392076913	–0.049740767	–0.392076913	–0.049740767
Acute teeth	0.465859736	0.077172692	6.036587832	1.01716E–08	0.31347959	0.618239883	0.31347959	0.618239883
L:W 2–3:1	0.344717254	0.132345487	2.604677057	0.01004104	0.083396519	0.606037989	0.083396519	0.606037989
L:W 3–4:1	0.788306049	0.21370129	3.688822128	0.000306088	0.36634547	1.210266628	0.36634547	1.210266628
Elliptic	0.638239383	0.111629389	5.717485238	4.99332E–08	0.417823299	0.858655467	0.417823299	0.858655467

ENTHALPY

SUMMARY OUTPUT

Regression Statistics	
Multiple R	0.940718428
R Square	0.88495116
Adjusted R Square	0.875544651
Standard Error	0.508639286
Observations	173

ANOVA

	df	SS	MS	F	Significance F
Regression	13	316.4127567	24.33944283	94.07859666	1.38084E–67
Residual	159	41.13551378	0.258713923		
Total	172	357.5482705			

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%	Lower 95.0%	Upper 95.0%
Intercept	27.05948184	5.745735614	4.709489552	5.37664E–06	15.71167597	38.40728771	15.71167597	38.40728771
Lobed	0.015247777	0.01005838	1.515927677	0.131523194	–0.004617485	0.035113039	–0.004617485	0.035113039
No Teeth	0.061429479	0.05666329	1.084114218	0.279955306	–0.050480303	0.173339261	–0.050480303	0.173339261
Round teeth	0.016236631	0.056536488	0.28718853	0.774341901	–0.095422716	0.127895978	–0.095422716	0.127895978
Acute teeth	0.017073255	0.056741998	0.300892736	0.763889393	–0.094991974	0.129138483	–0.094991974	0.129138483
Leptophyll 1	–0.023339139	0.010815362	–2.157961832	0.032431677	–0.044699438	–0.00197884	–0.044699438	–0.00197884
Leptophyll 2	–0.020874346	0.011209719	–1.862165047	0.064425241	–0.043013497	0.001264805	–0.043013497	0.001264805
Mesophyll 2	0.039227099	0.014028213	2.796300473	0.005807001	0.011521432	0.066932767	0.011521432	0.066932767
Emarginate apex	0.025664439	0.005367982	4.781021798	3.94572E–06	0.015062695	0.036266183	0.015062695	0.036266183
Attenuate apex	0.00839957	0.004349369	1.931215643	0.055235169	–0.000190418	0.016989558	–0.000190418	0.016989558
Round base	–0.010461803	0.004718911	–2.216995081	0.028042221	–0.019781635	–0.001141971	–0.019781635	–0.001141971
L:W <1:1	–0.042920589	0.011465711	–3.743386615	0.00025329	–0.065565324	–0.020275854	–0.065565324	–0.020275854
L:W 3–4:1	–0.019664129	0.010190647	–1.929625214	0.055433721	–0.039790617	0.000462359	–0.039790617	0.000462359
Elliptic	0.008798605	0.004906418	1.793284813	0.074828078	–0.000891552	0.018488762	–0.000891552	0.018488762