

PROCEEDINGS OF THE TWENTY-SIXTH ANNUAL KECK RESEARCH SYMPOSIUM IN GEOLOGY

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Students: *MOLLY REYNOLDS*, Franklin & Marshall College, *JACLYN WHITE*, Lafayette College, *LORELEI CURTIN*, Pomona College, *TYLER SCHUETZ*, Carleton College, *BRENNAN O'CONNELL*, Colorado College, *SHAWN MOORE*, Smith College.

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**Keck Geology Consortium: Projects 2012-2013
Short Contributions— Matanuska, Alaska Project**

GEOLOGY, PALEOECOLOGY AND PALEOCLIMATE OF THE PALEOGENE CHICKALOON FORMATION, MATANUSKA VALLEY, ALASKA

Faculty: *CHRIS WILLIAMS*, Franklin & Marshall College, *DAVID SUNDERLIN*, Lafayette College.

CLIMATE AND PLANT INTERACTIONS IN AN ANCIENT ALASKAN RAINFOREST

MOLLY REYNOLDS, Franklin and Marshall College

Research Advisor: Christopher Williams

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Research Advisor: David Sunderlin

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Research Advisor: Bosiljka Glumac

CLIMATE AND PLANT INTERACTIONS IN AN ANCIENT ALASKAN RAINFOREST

MOLLY REYNOLDS, Franklin and Marshall College
Research Advisor: Christopher Williams

INTRODUCTION

Ecosystem response to projected climate change is uncertain. However, the fossil record can inform us about the nature of ecosystems under past greenhouse climates. The study of the size and shapes of leaves (i.e., leaf physiognomy) is frequently used as an indicator of climate (Royer, 2012). Analyses of leaves in modern forests have indicated correlations between the characteristics of a leaf assemblage and climate that can be applied to paleofloral collections. For example, leaves in climates with low moisture availability tend to be smaller and thicker (Givnish, 1987), whereas teeth on the leaf margin disappear in favor of a smooth margin as mean annual temperature (MAT) increases (Royer, 2012). The latter correlation led to the development of leaf-margin analysis (LMA: Wolfe, 1979; Wilf, 1997), an empirical approach used in determining paleotemperature.

Plant-insect interactions preserved in the fossil record also have implications for paleoclimate, although the relationships are debated. Coley and Aide (1991) showed that herbivory tends to increase as latitude decreases, a pattern that is at least partially explained by the effect of increasing temperature on the metabolic rate of herbivores (Brown et al., 2004). However, a modern forest showed the opposite trend, with less herbivory in lower latitudes (Adams and Zhang, 2009). Other paleofloral assemblages show a positive correlation between increased atmospheric $p\text{CO}_2$ and associated temperature rise, and herbivory frequency (Carrano et al., 2008; Wappler et al., 2012).

This study focuses on the plant-insect interactions and paleoclimate indicators in a paleofloral assemblage from the late Paleocene-early Eocene Chickaloon Formation, south-central Alaska. Intermittent periods of extreme warming such as the Paleocene-Eocene Thermal Maximum (PETM, ~55 Ma) were superimposed on background global “greenhouse” conditions during this period in Earth’s history. In some lower latitude North American plant fossil assemblages, an increase in the number of plant taxa as well as an increase in the frequency of insect herbivory at the PETM have been attributed to the direct and indirect effects of elevated atmospheric CO_2 concentrations and temperatures (Carrano et al., 2008). Data from higher latitude North American fossil localities is more limited. Sunderlin et al. (2011) collected the first stratigraphic- and age-constrained fossil leaf collection from the Chickaloon Formation and performed the first study of early Eocene plant-leaf interactions at high latitudes.

Surprisingly, the paleoclimatic conditions of the early Eocene Chickaloon are not strikingly different from nearly coeval deposits from which significantly higher leaf damage frequencies are reported. MAT was estimated to be 16.4°C from an early Eocene bed in Carrano et al. (2008) compared to 11-14.6°C in Sunderlin et al. (2011). To investigate whether or not low incidences of leaf herbivory are unique to the previously sampled locality in the Chickaloon Formation, I excavated and sampled fossil leaves from a new Chickaloon locality.



Figure 1. Exposure of the Chickaloon Formation at Coyote Lake, near Sutton, Alaska. Arrow indicates location of MR fossil leaf layer.

METHODS

Geologic Background

The Chickaloon Formation was deposited in fluvial conditions in the Matanuska Valley-Talkeetna Mountains forearc basin in south-central Alaska (Trop et al., 2003). I sampled fossil leaves from a new locality at Coyote Lake, located north of Sutton, Alaska (61.74222°N, 148.89865°W). Coyote Lake is a reclaimed coal mine (the Mrak Mine) that was converted into a public-use area in 1987 (Hulen, 1987). Features of the Coyote Lake outcrop include coal beds, fossil wood, and scattered occurrences of leaf fossils in siltstones. One siltstone layer (“MR,” see Williams & Sunderlin, this volume) contained enough fossil leaves to sample (Fig. 1). Zircons from an ash located above the MR larger were dated to 55.3 ± 0.77 Ma (Curtin, this volume). Ash layers in the Evan Jones locality date the upper section of the Chickaloon to between 53.3 ± 1.5 Ma and 55.8 ± 1.7 Ma, suggesting that the PETM lies within that section (Triplehorn et al., 1984). The stratigraphic relationships of prominent coal beds also suggest that the coyote Coyote Lake outcrop lies stratigraphically downsection from the Evan Jones mine outcrop (Barnes and Payne, 1956). These data suggest that the leaves collected in this study site are late Paleocene or early Eocene in age.

Data Collection

A single horizon of siltstone was quarried for 543 fossil leaves. Per the methods of Currano et al. (2008), every angiosperm preserved with half of the leaf or greater was scored for insect damage. Leaves were scored regardless of the degree of preservation. Damage type (DT) classifications were based on Labandeira et al.’s “Guide to Insect (and Other) Damage Types on Compressed Plant Fossils” (2007). During collection, each fossil analyzed for damage was categorized into Raunkiaer-Webb size categories (megaphyll, mesophyll, notophyll, microphyll, nanophyll, or leptophyll; Raunkiaer, 1936), assigned a morphotype, and photographs were taken. Leaves with evidence of insect damage were transported back to the lab for further study. Currano et al.’s (2008) method of scoring leaves was used because having at least a half leaf makes it easier to assign a morphotype, and therefore the ability to determine morphotype-specific relationships. It also allows statistics on the proportions of morphotypes to be calculated.

Damage was classified as one of six functional feeding groups: (1) external foliage feeding, (2) piercing-and-sucking, (3) galling, (4) leaf-mining, (5) seed predation and (6) oviposition (Labandeira et al., 2007). External foliage feeding is further divided into hole feeding, margin feeding, skeletonization, and surface feeding (Labandeira et al., 2007). Labandeira et al. (2007) assigned a host specificity score to each DT based on patterns of insect feeding in modern forests and in the fossil record. A value of 1 is assigned to the most generalized type of feeding in which unrelated plants are consumed, a value of 3 is specialized feeding on only one or a few related species of plants, and a value of 2 is intermediate specialization (Labandeira et al., 2007).

Analyses

The leaf assemblage was analyzed using three physiognomic techniques: Leaf Margin Analysis (LMA: Wolfe, 1979; Wilf, 1997), Provisional Leaf Margin Analysis (PLMA: Kowalski and Dilcher, 2003), and Leaf Area Analysis (LAA: Wilf et al., 1998). A positive relationship exists between MAT and the proportion of sampled leaf morphotypes with entire margin leaves. Both LMA and PLMA exploit this relationship to empirically estimate paleo-MAT. Likewise, LAA

uses the relationship between leaf area and climatic conditions, specifically precipitation, to predict mean annual precipitation (MAP) from the average leaf area of an assemblage. In general, smaller leaves can better tolerate drought than large leaves (Royer, 2012). One commonly applied multivariate technique, CLAMP (climate leaf analysis multivariate program) (Wolfe et al., 1993), uses the site mean of 31 leaf characteristics to estimate MAT and other variables (Royer, 2012). Royer (2012) and others found that the estimates of MAT and MAP from CLAMP were no better than estimates from LMA and LAA. The statistical accuracy of CLAMP decreases significantly with fewer morphotypes, thus this collection was not a good candidate for CLAMP analysis.

RESULTS

Paleoclimate

Based on LMA and PLMA, MAT estimates from the Coyote Lake assemblage varied between 12.5 and 15.7°C. LMA generated the cooler temperatures (12.5 ± 3.8°C) and PLMA the warmer ones (15.7 ± 4.6°C). MAP, estimated from LAA, was 197.1 cm/yr (137.6-282.2 cm/yr).

Morphotype	Number of Specimens	Leaf Margin Score (<i>P</i>)	MlnA
A	63	0	8.28
<i>Grewiopsis auriculaecordatus</i>	86	0	9.03
<i>Dicotylophyllum richardsoni</i>	54	0	8.22
<i>Zizyphoides flabella</i>	127	0.5	7.75
E	10	1	8.04
<i>Carya antiquorum</i>	28	0	7.83
<i>Dicotylophyllum alaskana</i>	51	0	9.41
H	23	0	9.36
I	14	0	8.60
J	8	1	7.45
<i>Joffrea sp.</i>	30	0	8.25
<i>Aesculus hickeyi</i>	34	0	8.61
M	13	1	8.29
N	1	1	6.51
O	1	1	8.01

P = 0.37 Avg. = 8.24

Table 1. Frequency, leaf margin score, and MlnA (mean natural logarithm of leaf area) for each dicot leaf morphotype from the Coyote Lake exposure of the Chickaloon Formation, Alaska. Morphotypes that are not taxonomically defined are given letter names.

Leaf Diversity

The 543 samples from the Coyote Lake quarry yielded 15 discrete dicot morphotypes (Table 1). The large range of error in paleoclimate estimates is at least partially due to the low diversity of the leaf bed. The degree of preservation varied greatly among the samples, but many showed higher-order venation. Previous collections from the Evan Jones mine exposure generally have a greater degree of preservation than the collection described here. *Zizyphoides flabella* was the most commonly observed taxa (23%). In order to compare the morphotype diversity to other Chickaloon assemblages, a rarefaction curve was produced using DiversityAS software (Holland, 2008). The curve (Fig. 2) shows that 543 samples was a reasonable collection size to accurately describe the number of species present, and that it is unlikely that many more species would be found if sampling had continued. Compared to other Chickaloon beds, this collection reached its peak richness faster.

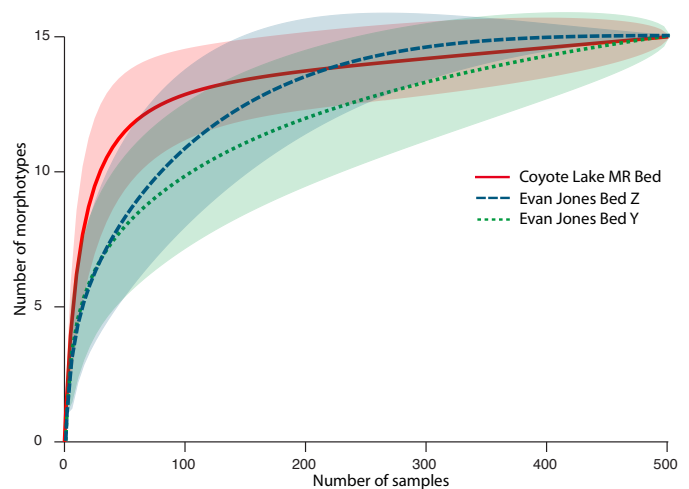


Figure 2. Rarefaction plant species curves for this collection (red), and two Evan Jones beds (blue, green) (Brannick et al., 2012). Analyzed in DiversityAS software (Holland, 2008, <http://www.huntmountainsoftware.com>).

Leaf Insect Damage

Of the 543 dicot fossil leaf samples, 29 exhibited at least one form of damage (5.3%). Nearly all (90%) of those were damaged in only one way, with 10% damaged in two ways. Hole feeding was the most common functional feeding group, with a majority of damaged leaves or leaf fragments ($n = 15$) damaged this way (Fig. 3a,b). Skeletonization was the second most common feeding group observed (10 instances of damage; Fig. 3d). Margin feeding, galling, and mining were also present in rare instances in the collection ($n = 3, 2, 1$, respectively; Fig. 3f,c,e).

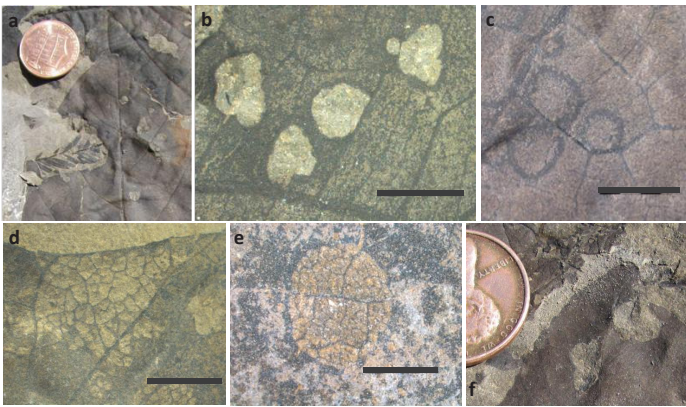


Figure 3. Representative insect feeding groups on Coyote Lake leaves, Chickaloon Formation, Alaska. (a,b) Hole feeding, (c) galling, (d) skeletonization, (e) mining, (f) margin feeding. (Scale bars: 4 mm.)

DISCUSSION

Paleoclimate

The results of my paleoclimate analyses indicate the Coyote Lake paleoenvironment was warm and wet compared to present day conditions in Alaska. Ash layers date Coyote Lake to slightly older than E3, but the paleoclimate estimates are very similar. The estimated MAT from Coyote Lake is slightly higher but within the range of possible MATs of the Evan Jones locality (Table 2). The fossil beds sampled at both Coyote Lake and Evan Jones are from floodplain lithofacies with meandering channels and overbank deposits (Neff et al., 2011) and contain abundant fossil plant remains consistent with wetland and riparian conditions. With these facts in mind, the PLMA regression (Kowalski and Dilcher, 2003), which is calibrated with modern wetland vegetation assemblages, is probably the more appropriate model for MAT estimation. Therefore, MAT was likely closer to $15.7\text{ }^{\circ}\text{C} (\pm 4.6\text{ }^{\circ}\text{C})$ for Coyote Lake.

MAP estimates for Coyote Lake indicate a climate with significant rainfall (197.1 cm/yr). This range overlaps with the high end of estimates for younger Chickaloon deposits (Sunderlin et al. 2011), but is much higher than MAP estimates from lower latitude Eocene deposits in North America (Table 2). Interestingly, my MAP estimates are more in line with paleoprecipitation estimates from middle to late Paleocene fossil deposits from the Canadian Arctic (Greenwood et al., 2010) than from lower latitude sites.

Locality	Age	Age (Ma)	Damaged (%)	MAT estimate $^{\circ}\text{C}$	MAP estimate (cm/yr)
Chickaloon, AK	late Paleocene-early Eocene	55.3	5.34	12.5-15.7	197.1
Bighorn Basin, WY (Wing et al., 2005)	~PETM	55	33	19.8	120
Chickaloon, AK (Brannick et al., 2012)	early Eocene	54.8	7.6	11-14.6	154.6
Chickaloon, AK (Sunderlin et al., 2011)	early Eocene	54.8	9.4	11-14.6	154.6
Republic, WA (Royer et al., 2007)	late early Eocene	49	49.8	13	>100
Bonanza, UT (Royer et al., 2007)	early middle Eocene	47.3	19.4	15	~84
Green River, CO (Smith, 2008)	middle Eocene	43-47	34*	16-23	~45-86
Florissant, CO (Smith, 2008)	late Eocene	34.1	23*	10.8-17.5	50

Table 2. Damage frequency, mean annual temperature (MAT), and mean annual precipitation (MAP) estimates for seven fossil leaf collections from North America. Results from this study are in bold.

* Damage rates from Smith (2008) were calculated as the percent of area damaged out of the total area of all leaves with at least 1 cm^2 preserved.

Leaf Diversity

The low number of distinct angiosperm morphotypes ($n = 15$) found in the leaf bed is not unusual for the Chickaloon Formation (Brannick et al., 2012), but is lower than expected for warm temperate forests in general. Species evenness is the relative abundance with which each species is represented in an ecosystem. The asymptotic nature of the rarefaction curve for this collection implies that few additional morphotypes would have been found if sampling had continued (Fig. 2). The most common morphotype in this collection, *Zizyphoides flabella*, was found in all beds in Sunderlin et al. (2011). The Coyote Lake outcrop represents a different microenvironment than the Evan Jones exposure, and therefore the diversity of morphotypes compared to other beds in the Chickaloon may be due to differences in how local vegetation was preserved in the fossil record (Sunderlin et al., 2011).

Insect Damage

Herbivory frequency is positively correlated with both temperature and precipitation, a relationship that is not explained by the comparatively high MAT and MAP of this assemblage (Wilf et al., 2001) (Table 2). Paleocene leaves from Currano et al. (2008) exhibited 15-38% of leaves damaged, which increased to 57% for PETM leaves. A study from central Europe compared leaf diversity and damage frequency of the Messel (47.8 Ma) and Eckfeld (44.3 Ma) deposits (Wappler et al., 2012). The Eckfeld deposit had significantly lower leaf diversity (33 morphotypes) and damage frequency (10.9%) than at Messel (93 morphotypes, 20.7% damaged) (Wappler et al., 2012). In modern subtropical forests in China, it was found that herbivory frequency increased with plant species richness after confounding characteristics were considered (Schuldt et al., 2010). Therefore, these data suggest that neither MAT nor MAP had a strong influence on herbivory frequency at the time of deposition, but rather that the low herbivory is related to the low plant diversity. The low plant diversity may be caused by poor soil nutrition (Wappler et al., 2012) or be related to the dynamic, high disturbance environment of the Chickaloon (Neff et al., 2011).

It has been suggested that low herbivory frequency is

related to the light regime at high latitudes. Extreme seasonality may cause lower insect survival rates, and thus lower insect herbivory (Coley and Aide, 1991; Brannick et al., 2012). Due to similarities with other paleofloral collections, it is more likely that the low herbivory in this collection is related to low plant diversity.

The varieties of DTs in five functional feeding groups suggest a diverse population of insect herbivores. The type of damage is indicative of the mouthparts of the insect. Hole feeding, margin feeding, skeletonization, and mining DTs are caused by insects with chewing mouthparts, such as beetles and caterpillars (Barbercheck, 2011). Galls are thought to give the insect better nutrition and a favorable microclimate, and can be caused by a variety of organisms, with gall midges, eriophyid mites, and aphids being the most common culprits (Knor et al., 2013). The highest frequencies of galling occur in arid to semi-arid conditions (Knor et al., 2013); thus, the wet warm temperate climate of the Chickaloon may explain the observed low frequency of galling.

Hole feeding (DT01, DT02) and skeletonization (DT16), which together make up 80% of the instances of damage at Coyote Lake, both have a host specificity score of 1, suggesting that most of the insect herbivores present at the time of deposition were generalists (Labandeira et al., 2007). Hole feeding and margin feeding were the most common feeding groups present in Sunderlin et al. (2011).

CONCLUSIONS

This study focused on comparing a new leaf bed in the Chickaloon to previous studies to explore how lithospacial variation might influence climate and leaf damage. Despite collection in geologically older strata, paleoclimate estimates are similar to previous studies, suggesting a long period of climatic and floral stability despite dynamic climatic conditions at the PETM. Limited herbivory is also consistent with previous studies, but is unusual in the greater picture of the late Paleocene-early Eocene greenhouse climate. Finding the PETM in the Chickaloon could provide better insight into any short-term changes in plant or animal composition. Studies of past greenhouse climates could provide insight into how current ecosystems will

adapt to increasing temperatures at the high latitudes.

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