

**KECK GEOLOGY CONSORTIUM**

**PROCEEDINGS OF THE TWENTY-SECOND  
ANNUAL KECK RESEARCH SYMPOSIUM  
IN GEOLOGY**

April 2009  
Franklin & Marshall College, Lancaster PA.

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(GRENVILLE PROVINCE, NEW YORK)**

Faculty: *WILLIAM H. PECK*, *BRUCE W. SELLECK* and *MARTIN S. WONG*: Colgate University

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

Students: *GARRISON LOOPE*: Oberlin College; *DOUGLAS MERKERT*: Union College; *JOHN LINDEN NEFF*: Amherst College; *NANCY PARKER*: Lafayette College; *KYLE TROSTLE*: Franklin & Marshall College; *BEVERLY WALKER*: Colgate University

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CHANGE**

Faculty: *JOHAN C. VAREKAMP*: Wesleyan University and *ELLEN THOMAS*: Yale University & Wesleyan University

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Short Contributions – Alaska**

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ALASKAN FORESTS, MATANUSKA VALLEY, ALASKA**

**Project Faculty:** *DAVID SUNDERLIN*: Lafayette College

**Project Faculty:** *CHRISTOPHER J. WILLIAMS*: Franklin & Marshall College

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**NANCY PARKER**: Lafayette College

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**BEVERLY WALKER**: Colgate University

Research Advisor: Connie Soja

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# A STUDY OF PLANT-INSECT INTERACTIONS IN THE PALEOCENE-EOCENE CHICKALOON FORMATION: PALEOECOLOGIC, PALEOCLIMATIC, AND PALEOLATITUDE IMPLICATIONS

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NANCY PARKER: Lafayette College  
Research Advisor: David Sunderlin

## INTRODUCTION

A pair of notable warm phases in earth history are the Paleocene/Eocene Thermal Maximum (PETM) and the Early Eocene Climatic Optimum (EECO). Signatures of this warmth have been noted across the globe in the marine and terrestrial fossil as well as the geochemical record (Kennet and Stott, 1991; Robert and Kennet, 1994; Sluijs et al., 2006; Zachos et al., 2006). Terrestrial ecosystem dynamics among plants and insects have been explored in the Big-horn Basin across the PETM and indicate that increased temperature and CO<sub>2</sub> resulted in increased herbivory (Currano et al., 2008). Here we report on a new plant-insect interaction dataset from a fossil leaf assemblage in the Late Paleocene/Early Eocene Chickaloon Formation in south-central Alaska.

The Chickaloon Fm. is a fluvio-lacustrine depositional sequence exposed in the Matanuska Valley. This unit preserves numerous foliage morphotypes (see Loope, this volume), many of which show evidence of insect damage. In a collection of >600 leaf specimens gathered from the Evan Jones Mine locality (see Williams & Sunderlin, this volume), ~9% showed at least one type of damage. Individual specimens in our collections exhibit margin feeding, hole feeding, leaf mining, and/or skeletonization. These data provide valuable insight into complex paleoecological interactions among trophic levels in the Chickaloon and may prove to be part of a dataset that can be used to test models of the paleo-latitude of deposition. Coley's (1991) research of modern forests concluded that high latitude correlates with decreased herbivory. Wilf (2008) also recognized that latitude is negatively correlated with insect damage. He also suggests that temperature

plays a major role in the incidence of herbivory, concluding that insects prefer warmer temperatures, a point that was reiterated by Coley (1999). If the Chickaloon assemblage is shown to have been deposited in a high-latitude setting, the flora allows for examination of latitudinal effects on plant-insect interactions in the Paleogene, perhaps dealing with season severity and plant response to unique high-latitude seasonal light conditions.

## MATERIALS AND METHODS

Our project's collection of leaf megafossils from the Chickaloon Formation was focused primarily on whole leaves, but for purposes of analyzing leaf damage, any leaf fragment greater than 1 cm<sup>2</sup> (damaged or not) was considered. This made it possible to compare our results with those of the Eocene Green River and Florissant Formations previously reported on by Smith (2008) and the Eocene Big-horn Basin (Currano et al., 2008). Additionally, it served to determine whether this site is worthy of further investigation on a bed by bed basis for changes in herbivory intensity and type.

The first goal of the study was to identify damage to the leaf during its lifetime (as opposed to taphonomic process damage) and describe damage types (guilds) and their relative abundances/frequency. Identifying specialized damage, damage that is induced distinctly by herbivores, is the first step. Reaction tissue is an indicator of damage on a leaf during its life on the tree. It is generally a ring of dark tissue around the damaged area (Figure 1A). This is a result of the plant attempting to heal following a feeding event or some other cause of damage

(Smith, personal communication). Reaction tissue is important because it shows that the leaf was alive at the time of feeding. Identifying this feature is especially useful in the case of hole feeding (Figure 1A) because though it is sometimes difficult to identify this feeding guild, reaction tissue is often visible, even in photographs. If reaction tissue is not present, one must make educated guesses based on the shape of the damage, its placement relative to the leaf venation, and the conditions of preservation of the particular specimen.

Generally, perfectly circular excisions were classified as hole feeding as these shapes are not likely to occur in early phases of decay and diagenesis. Leaf mining (Figure 1B) and skeletonization (Figure 1C) are more obvious leaf damage guilds although sometimes skeletonization can be confused with early decay patterns in the preservation of the leaf. This was easy to identify in our samples because the sample exhibiting skeletonization had small patches of removed tissue while the rest of the leaf lamina was well preserved.

The last guild, margin feeding (Figure 1D), is the excision of tissue around the margin of the leaf. It can be difficult to distinguish from hole feeding in some leaves. In many cases, however, feeding along the margin shows a circular form which can also be interpreted as hole feeding that has extended to the margin. This is different from insects feeding from the outside-in and so we had to determine whether the damage was originally hole feeding and happened to remove tissue along the margin or if they were originally chewing along the margin and working their way in as in true margin feeding (Labandeira et al., 2007).

Overall, there are probably many interpretations of what is and is not damage and how it should be classified and so the process is, admittedly, subjective with some specimens. It is necessary to be consistent once deciding how to classify the damage and, for the purpose of this study, it is crucial that we are consistent with Smith's (2008) interpretations in order to compare data and compile meaningful results. I was in consultation with Dr. Smith on a number of

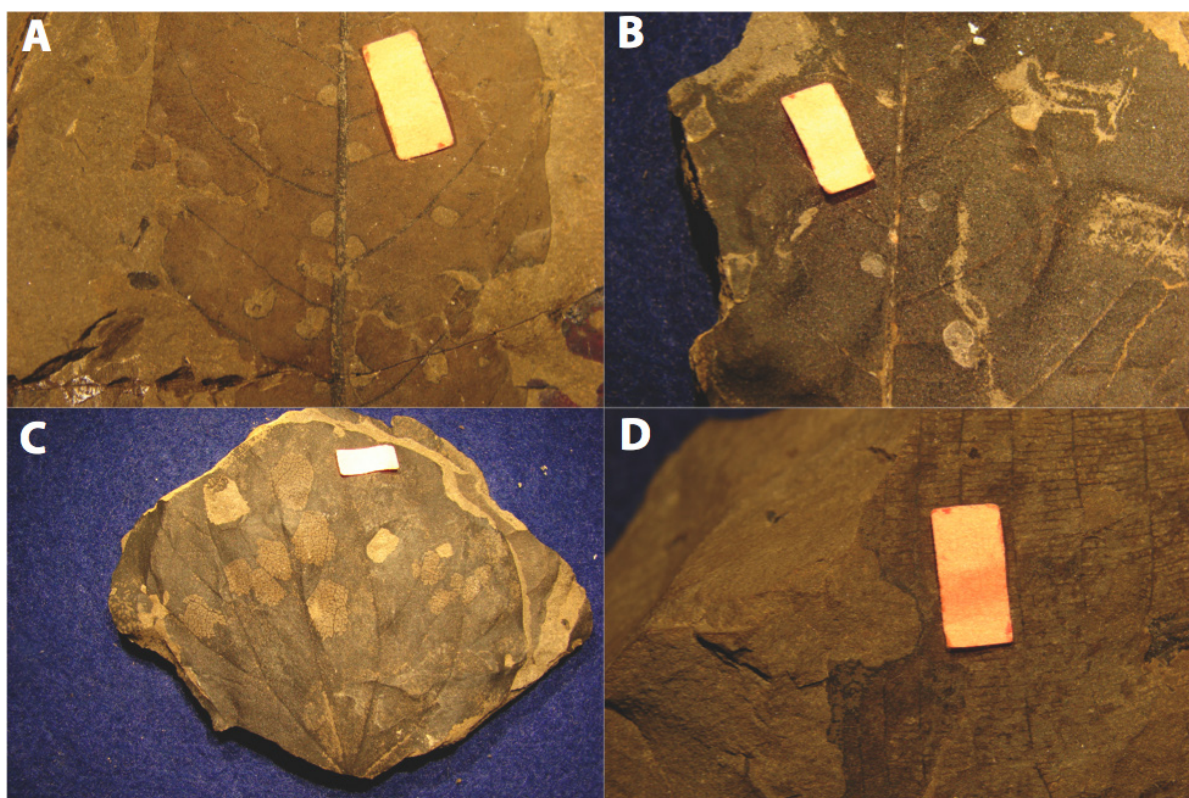


Figure 1. Photographs of the various damage types found within the Chickaloon Fm. A – hole feeding, B – leaf mining, C – skeletonization, D – margin feeding.

occasions to make sure this was so.

The total area of all leaves collected from the Chickaloon Fm. was calculated in EasyDraw, a program used for creating figures or drawings. The program also provides morphometric data of leaf area and damage shape. To do this I inserted specimen photos and adjusted the size of the image while constraining proportion so that each leaf was displayed to scale. EasyDraw calculated the area from a polygon drawn around the original area of the leaf. The area damaged was calculated in the same manner by drawing additional polygons and adding up the total area that was removed by insect damage. The total area damaged is a minimum estimate in most cases. These numbers were then converted to percentages (see Table 1) for comparison with data from Smith (2008) and Currano et al. (2008). Mean leaf area and mean leaf area damaged were also calculated and are shown in Table 1. Like Smith (2008), standard error was calculated to visualize how these values deviate from the mean.

Locality	Mean leaf area	Standard Error	Mean leaf area damaged	Standard Error	Damaged (%)
Florissant (n=624)	399.96	16.97	5.64	1.02	1.4
Green River (n=584)	434.73	23.12	10.95	1.49	2.5
Chickaloon (n=669)	1359.32	51	6.5	1.87	0.48

Table 1. Mean leaf area with mean leaf area damaged. Each locality is listed and the number of leaves in each collection is indicated. Standard error is shown for both mean leaf area and mean leaf area damaged. The percentage of total leaf area damaged is indicated in the far right column.

## RESULTS

Of the total number of specimens collected (n=669), ~9% exhibit damage of some form. This is significantly lower than the damage percentages of Smith's (2008) Green River and Florissant collections with (34% and 23% respectively) and Currano et al.'s (2008) Bighorn Basin collection (33%), all shown in Figure 2. Figure 3 shows the relative percent of feeding guilds for the Florissant, Green River, and Chickaloon collections. There is a noticeable dif-

ference in the distribution of damage types with the Chickaloon Fm. dominated by hole feeding whereas in the other collections hole feeding makes up the majority of the damage types but does not dominate to the same extent. Instead, margin feeding plays a much larger role and almost matches hole feeding in the Green River collection. There is a greater incidence of skeletonization and galling in both the Florissant and Green River formations as well.

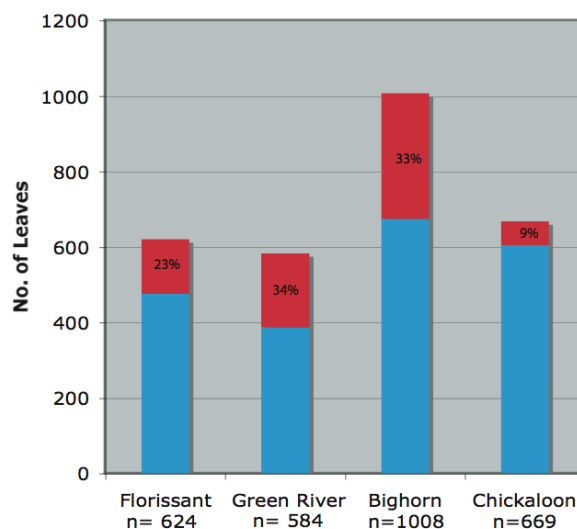


Figure 2. Leaf damage frequency among the four collections. Red indicates the % damaged. The number of leaves represents total number of specimens for each collection. Florissant and Green River data from Smith (2008) and Bighorn Basin data from Currano et al. (2008).

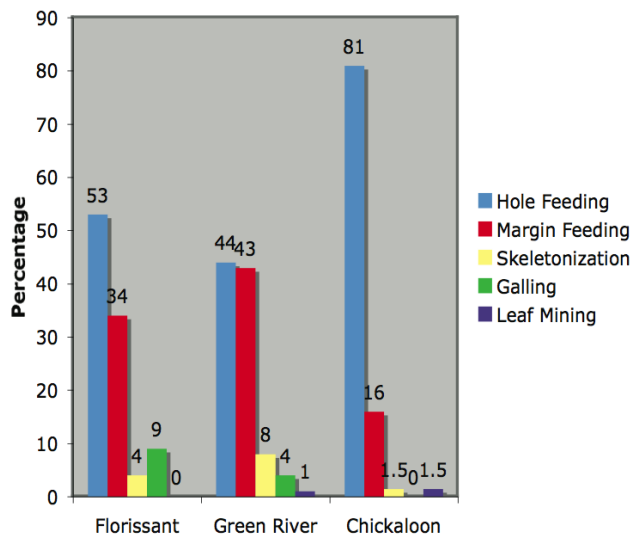


Figure 3. Distribution of damage types (guilds) within the Florissant, Green River, and Chickaloon collections. Percentages are shown above each bar.

Figure 4 shows graphically the percentage of total leaf area that was damaged in the three collections and includes the mean leaf area in mm<sup>2</sup> as well as the total percentage of leaf area that was damaged. The percentage of area that is damaged is significantly lower in the Chickaloon Formation (<0.5%). Interestingly, the mean leaf area for the Chickaloon was significantly higher than that of the other two sites. A larger standard error for this value also means that there is a larger deviation in the size of leaves that were collected from our site. The standard error for mean leaf area damaged differs greatly among the sites as well. The standard error for the Chickaloon Fm. is more than double the standard errors for the other two localities indicating that there was great variability in the intensity of damage on a leaf at our site even though fewer leaves were herbivorized overall.

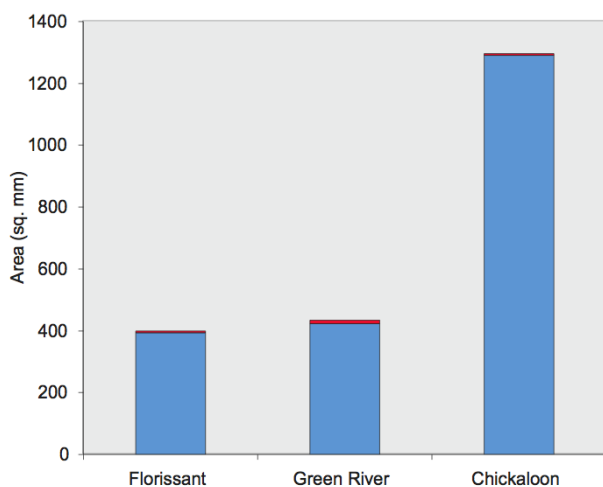


Figure 4. Compares the total area (sq. mm) damaged in each of the collections. The red represents the total area damaged.

## DISCUSSION

Compared with coeval lower latitude sites in Colorado and Wyoming, the Chickaloon paleoflora is relatively “pristine” in the leaf herbivory sense with only ~9% of leaves collected in the Chickaloon Formation exhibiting damage of any type. This may be due to several factors. The one factor that we are most interested in is latitude. Phyllis Coley has provided evidence for a latitudinal gradient in her studies of modern plant-insect interactions (Coley,

1991). Wilf (2008) provides three hypotheses related to herbivory, the first being that the frequency of herbivory is correlated with temperature. As we know, lower latitudes receive more direct sunlight and therefore are warmer than higher latitude locations. Another possible explanation for the decreased herbivory is seasonality. Alaska experiences severe winters and shorter summers than lower latitude localities. Also, warm weather that attracts herbivores begins later in the year. As insects either migrate north at the end of the winter or hatch in springtime weather conditions, they may appear in Alaska much later after they have already begun feeding at lower latitudes. This shorter feeding time may result in a lower percentage of feeding overall. Seasonality also affects leaf growth in general. If the season is shorter at higher latitudes, then it will also take until later in the year for leaves to grow to their full size. If the timing of spring hatch and leaf budding and early growth is offset, the leaf damage frequency would likely be altered toward the lower end. Precipitation rates may also be involved in producing the low incidence of herbivory in Early Eocene Alaska and work has begun in addressing how much rainfall southern Alaska experienced during this time.

The overwhelming majority of herbivory in the Chickaloon collection is hole feeding, followed distantly by margin feeding. However, there is little leaf mining and skeletonization and a complete absence of galling damage. This may be due to a lower diversity of insects at high latitudes. With fewer species there will likely be fewer damage types. Wilf (2008) suggests that feeding diversity increases with increased temperature because insect performance is enhanced. Even so, from our data we do not see much evidence for a latitudinal gradient within the guild distribution (see Figure 3). Skeletonization, leaf mining, and galling are not abundant in any of the collections. The diversity of herbivores may also be low due to a low diversity of host plants (Wilf, 2008).

## CONCLUSIONS

This is the first study of plant-insect interactions

from the Chickaloon Formation of Alaska and it has given us much insight into the Paleogene environment of the region. However, it is clear that there is much still to be investigated. One of the aspects about the Chickaloon Fm. that is the most intriguing is the variety of feeding types. Although the majority of damaged leaf area is represented by hole feeding and margin feeding, there are rare samples of skeletonization and leaf mining. It would be interesting to collect additional specimens exhibiting these types of damage to get a better sense of all the feeding guilds and their sub-types. We found that latitude does play a role in plant-insect interactions. Herbivory decreases with increasing latitude, both in frequency and diversity in the Recent and this study supports this notion in the Early Eocene as well. However, latitude is only one aspect of this investigation. It would be useful to analyze the data more thoroughly to determine how climate in general has affected herbivory within the Chickaloon Fm. A more thorough study of the Chickaloon Fm., like that of Currano et al. (2008) would incorporate a variety of beds before, during, and after the PETM.

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