PALEOCLIMATIC AND PALEOECOLOGICAL IMPLICATIONS OF A PALEOCENE–EOCENE FOSSIL LEAF ASSEMBLAGE, CHICKALOON FORMATION, ALASKA

DAVID SUNDERLIN,1* GARRISON LOOPE,2 NANCY E. PARKER,1,3 and CHRISTOPHER J. WILLIAMS4
1Lafayette College, Department of Geology and Environmental Geosciences, Easton, Pennsylvania 18042, USA; 2Oberlin College, Department of Geology, Oberlin, Ohio 44074, USA; 3University of Wisconsin, Department of Geography, Madison, Wisconsin 53706, USA; 4Franklin & Marshall College, Department of Earth & Environment, Lancaster, Pennsylvania 17604, USA
e-mail: sunderld@lafayette.edu

ABSTRACT
New collections of a leaf compression-impression paleoflora preserved in fluvo-lacustrine sediments of the upper Chickaloon Formation, south-central Alaska, United States, provide leaf physiognomic climate estimates for the early Eocene in southern Alaska and rare data on plant-insect interactions from a subarctic setting. Thirty-nine broadleaf angiosperm morphotypes occur in a paraautochthonous assemblage along with Metasequoia shoots and trunks, compressions of a diverse suite of seeds, monocotyledonous aquatic plants, freshwater gastropods, and inclusion-bearing dispersed amber. Leaf-character derived mean annual temperature estimates (11–14.6 °C) are significantly warmer than Alaska at present and indicate warm temperate conditions at the time of deposition. Leaf-derived mean annual precipitation estimates of ~110–160 cm/annum are comparable to those from similar-age paleofloras in Arctic Canada and indicate wetter conditions than nearby coeval paleofloras further south in the North American mid-latitudes. Leaf herbivory is rare in the Chickaloon assemblage (~9% of leaf fragments) as compared to other, lower latitude Eocene assemblages, but exhibits four of the main leaf-damage guilds (hole feeding, margin feeding, surface feeding, and skeletonization). These data provide a rare glimpse at a high-latitude terrestrial forested ecosystem during a global hothouse climate phase and thus have implications in understanding how biogeographic patterning and ecological systems respond to non-analog, warm high-latitude environmental conditions.

INTRODUCTION
A period of late Paleocene–early Eocene (~58–48 Ma) global warmth, including the Paleocene–Eocene Thermal Maximum (PETM), has been documented in the fossil and geochemical records by multiple marine and terrestrial paleoclimatic and paleoenvironmental studies (e.g., Kennett and Stott, 1991; Robert and Kennett, 1994; Markwick, 1998; Röhli et al., 2000, 2007; Zachos et al., 2001, 2003, 2006; Bowen et al., 2002; Tripati and Elderfield, 2005; Slujs et al., 2006; Yans et al., 2006; Weijers et al., 2007). Recent analyses of paleoflora and paleoclimates in mid-latitude North American basins indicate anomalously warm mean annual temperatures (MAT) and a positive correlation with the intensity of leaf damage by insects (Wing and Greenwood, 1993; Wing, 1998; Wilf and Labandeira, 1999, 2000; Wilf, 2000; Wilf, 2000; Fricker and Wing, 2004; Wing et al., 2005; Curran et al., 2008; Smith, 2008). Combined analyses using leaf physiognomic approaches to paleoclimatic and plant-insect interactions, however, are scarce from high-latitude North America during this time. Considering the well-supported and much-publicized sensitivity of polar and subpolar regions to climatic change (e.g., Holland and Bitz, 2003), high-latitude paleofloras are integral to our understanding of hothouse climatic conditions. The purpose of this study is to examine a rich high-latitude paleobotanical record from southern Alaska’s Paleocene–Eocene Chickaloon Formation for a coupled paleoclimatic and paleoecological analysis of its fossil leaf assemblage. As such, this paper represents the first analyses of stratigraphically tied, age-constrained fossil leaf collections from this unit and the first report of plant-insect interactions at high latitudes near the Paleocene–Eocene boundary. Investigation of these climate-ecosystem records is crucial in developing an understanding of the response of polar and subpolar terrestrial ecosystems to ancient warm climates. These systems provide a deep time context for future equable conditions at high latitudes and for vegetational changes that may lead to feedbacks to the atmospheric and global carbon balance.

GEOLoGIC SETTINg
Basin Development
The Cretaceous–Paleogene Matanuska Valley–Talkeetna Mountains forearc basin developed between a volcanic arc and an accretionary prism in association with subduction of the Kula and Farallon plates beneath the Wrangellia composite terrane (Tropl et al., 2003). Today, the basin is bounded on the north by the Castle Mountain Fault or the southern Talkeetna Mountains’ older Mesozoic strata, and to the south by the Border Ranges Fault at the Chugach Terrane accretionary complex’s northern suture. Paleocene to early Oligocene activity on these faults led to a fluvial basin inflow sequence, as braided and meandering stream systems deposited sediments from volcanioclastic and other source rocks from the Chugach accretionary complex onto the southern flanks of the basin. Ultimately these fluvial systems coalesced into a westward-flowing, meandering trunk river along the basin axis (Flores and Stricker, 1993; Trop et al., 2003; J. Neff, personal communication, 2011). Paleomagnetic analysis and inference of the paleolatitude of the Paleogene record of deposition in the basin, however, remains uncertain. Data from Hillhouse and Gromme (1982) suggested to Wolfe (1994) that Paleocene–Eocene deposition of rocks now exposed in the Matanuska Valley may have occurred as high as 76°N paleolatitude. On the other hand, low-latitude extreme, data analyzed by Stamatakos et al. (1988, 1989) and Hillhouse and Coe (1994) suggested that the basin’s late Paleocene–early Eocene strata were deposited perhaps ~1600 km (~1200 km) south of its present location (~62°N). The accuracy of these conclusions is suspect, however, considering that the same studies indicated that by 55–50 Ma, the basin had translated northward to near its present latitudinal position. Indeed, other paleomagnetic data of the southern Talkeetna Mountains’ Eocene Caribou Creek volcanics (Hillhouse et al., 1985; Panuska et al., 1990) indicate that no significant northward displacement for the Wrangellia composite terrane has occurred since ca. 55 Ma. These observations, combined with Cretaceous and early-middle Paleocene paleomagnetic data from Stamatakos et al. (2001) and new field geological relationships among rocks associated with the Caribou Creek volcanics, led Cole et al. (2006) to conclude that no more than 500 km (and probably ~200 km) of tectonic displacement has occurred to the Wrangellia composite terrane since 57 Ma.
Chickaloon Formation

The lowermost of the terrestrial sedimentary units that filled the Matanuska Valley–Talkeetna Mountains basin is the >1500-m-thick Chickaloon Formation. This unit comprises a complex succession of sandstones, laminated siltstones, mudstones, carbonaceous shales, coal beds, and conglomerates. Chickaloon strata lie in angular unconformable contact with the underlying Upper Cretaceous marine Matanuska Formation (Trop et al., 2003). Chickaloon lithofacies represent predominantly fluvial conditions sourced with sediments from the adjacent zones of uplift (Flores and Stricker, 1993; Trop et al., 2003; J. Neff, personal communication, 2011). The westernmost extent of the Chickaloon shows lithofacies characteristic of marginal marine settings (Trop et al., 2003) and thus the basin was likely at low elevation throughout its depositional history. As the basin filled, coarser alluvial deposits prograded across the paleovalley depositing the Wishbone Formation, which conformally overlies the Chickaloon Formation (Trop et al., 2003). Based on a composite collection of the formation’s well-preserved leaf megafossil assemblages, Wolfe et al. (1966) assigned a Paleocene age to the Chickaloon. K-Ar dating of plagioclase phenocrysts and fission-track dating of zircons from interbedded ash partings, however, show that the P-E boundary falls within the Premier Coal Zone in the upper 150 m of the formation (Triplehorn et al., 1984); the best age estimates to date, therefore, indicate that the unit straddles the P-E boundary. This age constraint, together with recent paleolatitude interpretations described above, also indicates that the sediments were deposited near their present day subpolar latitude north of 60°N.

The finer-grained lithofacies in the Chickaloon Formation, particularly those with carbonate cements, contain a well-preserved paleofloral assemblage including compression-impression dicot leaves, seeds, and flowers, as well as multiple species of cupressaceous conifers, ferns, and palms (Wolfe et al., 1966). The paleoflora shows a resemblance to the Fort Union Formation paleoflora in Wyoming, Colorado, Montana, and North Dakota, United States, and the Upper Atanikerdluk of northwestern Greenland, both of which have been well dated to the Paleocene (Heer, 1869; Koch, 1964; Wolfe et al., 1966; Wing et al., 2005). Many foliar elements are similar to the late Paleocene upper Sagwon paleoflora of the Prince Creek Formation (northern Alaska Peninsula) (Moiseeva et al., 2009). Due to the presence of palms and other taxa, Wolfe et al. (1966) suggested that the Chickaloon assemblage represented a warm temperate to subtropical floodplain forest, noting that as many as 50% of leaf fossil morphotypes exhibit entire margins. Wolfe (1994) performed a leaf physiognomic climate estimate analysis on this collection (Climate Leaf Multivariate Program; CLAMP) and obtained results that indicate wet and warm temperate conditions, corroborating earlier paleoclimatic interpretations. The composite collection in these analyses, however, includes samples from an unknown thickness of the Chickaloon Formation and from numerous localities scattered along the basin axis in the Matanuska Valley. Unfortunately, the precise stratigraphic location where these collections were made is not known. Until the present study, no analyses of stratigraphic- and age-constrained fossil leaf collections from the Chickaloon have yet been published.

The only faunal body fossils yet documented from the unit include the freshwater gastropod genera *Campeloma* and *Belliampya* (Viviparidae) (Wolfe et al., 1966; Walker, 2009) and a solitary occurrence of a nearly complete chelyrid turtle carapace (Hutchison and Pasch, 2004). Both occurrences support a forested floodplain and mire environment of deposition consistent with the interpretations of Flores and Stricker (1993) and Neff (J. Neff, personal communication, 2011).

### Evan Jones Mine Locality

Stratigraphically constrained fossil leaf collections were made at the Jonesville coal mining district on the Wishbone Hill Syncline northwest of Sutton, Alaska (61°44’ N, 148°57’ W) (Fig. 1). The mining region comprises several large, open pits that have been partially filled during recent reclamation. The largest of these pits, the Evan Jones Mine, is located on the northern slope of Wishbone Hill and reveals ~1000 m of continuous east-west lateral exposure and as much as 150 m of combined vertical section. The outcrop is broken by numerous small faults of tens of meters of offset that do not obscure stratigraphic relationships along laterally continuous beds (Fig. 2) (Flores and Stricker, 1993; J. Neff, personal communication, 2011).

The fluvial and lacustrine Chickaloon paleoenvironments at the Evan Jones Mine are evidenced by interbedded carbonaceous shale and sandstone lithofacies as well as many bituminous coal deposits (Flores and Stricker, 1993; J. Neff, personal communication, 2011) (Fig. 3). The lithofacies associations suggest a floodplain mire-dominated system with occasional channel and crevasse splay depositional events. The Eocene Wishbone Formation conformably overlies the Chickaloon at the site and is represented by polymict clast- and matrix-supported conglomeratic lithofacies interpreted to have been deposited in an alluvial fan setting (Trop et al., 2003).

### COLLECTIONS

Five collections of leaf compression-impression fossils were made from five distinct carbonate-cemented siltstone horizons (15–100 cm thick) at the Evan Jones Mine site. Each bed was sampled continuously over a lateral distance of ~10 m until the bed pinched out or became inaccessible on the outcrop (Fig. 2). Leaf collections were made to record the morphotype richness observed in the field and therefore do not constitute a quantitative collection of leaf abundance in any one bed. More than 1000 fossil leaf specimens were extracted in the field and a total of ~370 complete or mostly complete dicot specimens representing the total sampled morphotype richness were retained for study. Retained collections recovered from the four major beds (n = 75–121; herein labeled A, B, C, and D) (Fig. 3) yielded 39 leaf morphotypes (see Supplementary Data1). Of these beds only B and C yielded sufficient morphotype diversity to allow quantitative paleoclimatic analysis using leaf physiognomic characters. Bed E yielded substantially fewer samples (n ~ 20) with only five morphotypes, and these data were only included in composite analyses. Non-dicot foliar remains are abundant in floodplain and lacustrine facies throughout the study section and include shoots of *Metasequoia* and *Glyptostrobos* (conifers), the monocot *Haemanthophyllum*, and axes of the sphenophyte *Equisetites*.

The stratigraphically lowest sampled bed (A) was located about 10 m above the top of the Premier Coal Zone and the reported Paleocene–Eocene boundary (Triplehorn et al., 1984). No samples were taken from the Premier Coal Zone or below, as these strata were inaccessible at this outcrop due to mine reclamation backfill.

Discrete broadleaf morphotypes were distinguished by standard methods (Ash et al., 1999; Ellis et al., 2009) and when possible, we tentatively assigned distinct morphotypes to published genera and species using Wolfe (1966, 1977), Wolfe et al. (1966), Hickey (1977), Brown (1962), and Hollick (1936). Where we found insufficient evidence to confidently assign taxonomic names, morphotypes were assigned two-character identification codes in which the first half of the code signifies the bed where the morphotype was first cataloged, and the second indicates the arbitrary order in which the morphotype was cataloged within that bed (e.g., B10) (Table 1).

All study specimens were accessioned into the Earth Sciences collections at the Museum of the North, University of Alaska, Fairbanks (UAM.2008.001.ESCI).

---

1 http://palaios.ku.edu
ANALYSES

We employed four widely used leaf physiognomic analyses to estimate climatic variables from the Chickaloon assemblage: leaf margin analysis (LMA: Wolfe, 1979; Wing and Greenwood, 1993; Wilf, 1997), provisional leaf margin analysis (PLMA: Kowalski and Dilcher, 2001, 2003), the climate leaf analysis multivariate program (CLAMP: Wolfe, 1993, 1995; Wolfe and Spicer, 1999), and leaf area analysis (LAA: Wilf et al., 1998). We used these various analyses in order to provide paleoclimatic estimates across a wide spectrum of methodologies and to facilitate the comparison of the Chickaloon results with published paleoclimatic estimates.

Leaf Margin Analysis

Leaf margin analysis (LMA) utilizes the positive relationship between mean annual temperature (MAT) and the proportion (P) of sampled leaf taxa with entire margins from woody dicots in modern forests. The relationship was first noted by Bailey and Sinnott (1916) and has been supported by more recent quantitative studies (Wolfe, 1979; Wilf, 1997). Although the mechanism driving this smooth margin-MAT correlation is not yet fully understood, Royer and Wilf (2006) suggested that toothed margins increased transpiration and carbon uptake early in the growing season when temperatures are growth limiting, thus giving toothed leaves an advantage in cooler climates with short growing seasons. The LMA regression equation used in this study is based on a large data set of modern woody dicot leaf collections from across eastern Asia (Wolfe, 1979). In accordance with Wolfe (1979) and Wing and Greenwood (1993), we calculated the leaf-estimated mean annual temperature (LMAT) using $P$, the fraction of morphotypes with an entire margin ($LMAT(°C) = 30.6P + 1.14$). We counted the few morphotypes that had both entire and toothed forms as half entire (0.5 value). LMA was conducted on the two beds with sufficient morphotype richness (B and C) as well as all beds combined. Standard deviation was calculated using the number of morphotypes in the flora (Wilf, 1997):

$$\sigma[LMAT] = 30.6\sqrt{\frac{P(1-P)}{r}}$$

(1)

Provisional Leaf Margin Analysis

Provisional leaf margin analysis (PLMA) (Kowalski and Dilcher, 2001, 2003) considers a modern MAT to P regression ($LMAT(°C) = 36.3P + 2.223$) through modern leaf assemblages from exclusively riparian or wetland environments. While PLMA is based on a dataset from fewer modern forests than LMA, the method may be more appropriate for comparison with a paleofloral assemblage from similar depositional paleoenvironments such as that of the Chickaloon Formation (Flores and Stricker, 1993; J. Neff, personal communication, 2011). To find the standard deviation we used the equation from Wilf (1997) above (eq. 1) with the slope constant (36.3) of Kowalski and Dilcher (2003).
CLAMP

Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe, 1993; Spicer, 2009) attempts to produce more detailed climate estimates using leaf margin character and six additional dicot leaf characters (presence of lobes, leaf size, base shape, apex shape, length-to-width ratio, and blade shape). Canonical correspondence analysis is then applied to the climate and leaf data from a modern calibration dataset of 144 forests from across the Northern Hemisphere, predominantly in the temperate latitudes of North America and East Asia (Wolfe, 1995). Leaf physiognomic characters from fossil assemblages are then compared to this dataset. The accuracy of predictions for climate parameters at the time of fossilization deteriorates rapidly when less than 20 taxa are used, so we utilize this analysis only for those beds that yielded at least 20 morphotypes (Beds B and C) and the composite upper Chickaloon collection including all morphotypes in Beds A–E (n = 39).

CLAMP predicts a range of climatic variables including MAT, warm-month mean temperature (WMMT), cold-month mean temperature (CMMT), length of growing season (GRS), growing season precipitation (GSP), mean monthly growing season precipitation (MMGSP), precipitation during the three consecutive wettest months (3WET), precipitation during the three consecutive driest months (3DRY), relative humidity (RH), and specific humidity (SH). The method provides more accurate prediction ranges than can be considered in conjunction with the other techniques but, when predicting MAT, it is not necessarily more accurate than LMA (Jacobs and Deino, 1996; Wilf et al., 1998; Wing and Greenwood, 1993). Leaf area is related to water availability because large leaves have a greater surface-area-to-volume ratio than small leaves, and they lose water to transpiration more readily. For this reason plants in arid conditions tend to have small leaves while plants in moist areas more typically develop large leaves. Water availability for a plant is determined by many factors including precipitation, evapotranspiration, temperature, seasonality, and soil conditions (Wilf et al., 1998). Because of these numerous confounding variables, good estimates of water availability from leaf area translate into a first-order precipitation proxy.

Wilf et al. (1998) used data from 50 modern leaf collection sites across Central and South America to develop the MAP prediction equation:

\[
\ln[MAP(cm)] = 0.548 M[\ln A(cm^2)] + 0.768
\]

where \( M[\ln A(cm^2)] \) is the mean of the natural logarithm of the leaf areas for all morphotypes. In order to approximate \( M[\ln A] \) we used the equation:

\[
M \ln A = \sum a_i p_i
\]

where \( p_i \) represents proportions of morphotypes in each of seven Raunkiaer-Webb size categories (Raunkiaer, 1934), and \( a_i \) represents their respective natural logarithm leaf areas (2.12, 4.32, 6.51, 8.01, 9.11, 10.9, 13.1).

Standard error for \( \ln(MAP) \) is 0.359 for all LAA which, when calculated in terms of centimeters of precipitation, gives asymmetric error bars because the error is a natural logarithm. Wilf et al. (1998)
recommend that this technique be used only for sites containing at least 16 morphospecies. Thus, LAA was performed only on Beds B and C at our locality and the composite of all sampled beds (A–E) at the Evan Jones Mine.

Leaf Damage

A total of 669 dicot leaf fossil samples from Beds A–E were analyzed for leaf damage. This total included the leaf fossil collections for paleoclimatic analysis described above plus any leaf or leaf fragment on these same slab samples with an area $>1$ cm$^2$ (e.g., Smith, 2008). Because this sampling protocol utilized the same collection of samples for both analyses, we believe that this dataset is relatively unbiased toward damaged leaves and may be used in calculations of overall damage incidence in the paleoflora for comparison with data in Smith (2008). The leaf damage data are considered from all beds together as they were likely to have been deposited very close to each other in time (see above discussion of sedimentation rate). Both the total area of each leaf or leaf fragment and the foliar tissue damaged and/or removed by herbivory were calculated digitally using image analysis software (EasyDraw, ver. 3.5). All noted damage was identified to functional feeding groups and scored to damage type categories in Labandeira et al. (2007).

RESULTS

Composition

Chickaloon dicot leaf collections from the Evan Jones Mine yielded a total of 39 discreet morphotypes (Table 1) across all sampled beds (Fig. 2). Leaf margin characters are well-preserved in the assemblage and many specimens show higher-order venation (examples in Fig. 4).
Bed B yielded the highest richness with 22 dicot morphotypes, whereas Beds A, B, C, D, and E yielded 11, 21, 12, and 5 morphotypes each, respectively. Bed C had the most unique morphotypes (8), while Beds A, B, D, and E had 3, 6, 3, and 1, respectively. Although only *Zizyphoides flabella* was present in all sampled beds, many taxa are present in more than one bed.

**Paleoclimate**

Analyses of leaf margins yielded MAT estimates spanning from 11.0 to 14.6 °C for Beds B, C, and the composite and analysis of all collections together (A–E). LMA generated the cooler MAT estimates and PLMA the warmer ones (Table 2). These results corroborate the findings of an independent LMA on a separate composite collection from the same locality (12.3–13.5 °C, Sunderlin et al., 2007). When all morphotypes from all beds are combined, LMA predicts an MAT of 11.0 °C (±2.3 °C) whereas PLMA estimates a higher MAT of 13.9 °C (±2.7 °C). The CLAMP analysis generated little difference in all climate parameters among the analyzed assemblages (Beds B and C plus Composite) (Table 3). All estimates fall within one standard deviation of each other and overall the method produces smaller standard deviations than LMA, PLMA, or LAA. MAT estimates from CLAMP are consistently within the range of values predicted by LMA and PLMA (Table 2).

CLAMP also estimates a WMMT of ~22 °C and a CMMT of ~5.5 °C. The analysis predicts a growing season that lasted ~7.5 months with ~120 cm of precipitation, with the three wettest months receiving 64 cm, and the three driest months, 39 cm. These results are not dissimilar to the Wolfe (1994) CLAMP analysis of a similarly sized collection of 29 morphospecies which yielded a lower MAT (12.3 °C), a greater range of temperature, and higher precipitation estimates (145 cm growing season precipitation) (Table 3). LAA (Wilf et al., 1998) of collections from Beds B and C produced similar proportions of the different leaf-area classes; therefore, the method yielded similar MAP estimates (160.3 and 158.9 cm) (Table 4).

**Leaf Damage**

Of the total analyzed leaf-damage collection, 63 of 669 leaves or leaf fragments exhibited some form of damage. Of these, 51 (81%) were damaged in one way only, while the remaining 12 showed two forms of damage. The most common leaf functional feeding type present in the Chickaloon paleoflora is hole feeding; circular excisions that are clearly separate from feeding along the margin (Fig. 5A). The excisions are often concentrated in clusters but may also appear individually (damage types DT02 and DT04 of Labandeira et al., 2007). A total of 51 leaves or leaf fragments exhibited this type of damage.

Marginal feeding is the second most common functional feeding group observed (10 leaves or leaf fragments) and can be identified as excision along the margin of the leaf (Fig. 5D), indicating that the insect fed from the outside in toward the midrib. Often there are multiple locations along the leaf margin where this is evident. (DT12 of Labandeira et al., 2007))

Skeletonization (DT16) was present on only one Chickaloon specimen (*Zizyphoides flabella*) but is exquisitely preserved (Fig. 5B). Excision of the tissue clearly displays the inner higher-order veins of the leaf with only very poorly developed reaction tissue visible along the periphery of the damage. Surface feeding was exhibited by only one specimen in our collection (Fig. 5C; *"Simiwilsomia*’ sp.). This damage type is similar to DT30 (Labandeira et al., 2007) and does not occur on primary or secondary veins. Unaltered veins are visible through the feature indicating the absence of gall tissue.

**DISCUSSION**

The fossil leaf assemblage in the upper Chickaloon Formation at the Evan Jones Mine is superb in terms of preservation and abundance. The beds that were identified to be the most diverse for dicot leaves were selectively sampled in this study but many other *Metasequoia* or *Equisetites*-rich horizons occur frequently throughout the exposure. The apparently rapid sedimentation of the upper Chickaloon Formation (Flores and Stricker, 1993; J. Neff, personal communication, 2011) leads us to believe that differences in the distribution of morphotypes among beds (Table 1) are likely the result of local preservation of floodplain vegetation zones arrayed around a shifting stream course rather than the reflection of a time-transgressive change in local or regional climate. By extension, the composite collection may most fully reflect the leaf litter of the upper Chickaloon ecosystem with adequate sampling of the local flora and relatively little time averaging.

The abundance of the presumed aquatic genera *Equisetites* and *Haematophyllum* throughout the studied strata corroborates previous fluvial or wetland-mire depositional setting interpretations (Wolfe et al., 1966; Flores and Stricker, 1983; Trop et al., 2003; J. Neff, personal communication, 2011). The fine sediment matrix and nonfragmentary fossil preservation implies deposition in low-energy sites where leaf litter input from plants growing nearby resulted in an autochthonous or parautochthonous assemblage. Vertically oriented cupressaceous conifer stumps and logs (*Metasequoia*) occur *in situ* within the coal deposits between the studied beds (Williams et al., 2010), and we interpret the broadleaf remains to have been brought into *Metasequoia*-dominated mires from a local source during periods of flooding.

---

**TABLE 2**—Leaf margin data and analysis results for Evan Jones Mine collections in the Chickaloon Formation. P = proportion of leaf morphotypes with entire margins, LMAT = leaf-estimated mean annual temperature, LMA = leaf margin analysis (Wolfe, 1979; Wing and Greenwood, 1993), PLMA = provisional leaf margin analysis (Kowalski and Dilcher, 2003).

<table>
<thead>
<tr>
<th>Collection</th>
<th>Morphotypes</th>
<th>P</th>
<th>LMA (°C)</th>
<th>LMAT (°C)</th>
<th>PLMA (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>12</td>
<td>0.208</td>
<td>7.5 (3.59)</td>
<td>9.77 (4.25)</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>21</td>
<td>0.333</td>
<td>11.33 (3.14)</td>
<td>14.31 (3.73)</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>11</td>
<td>0.273</td>
<td>9.49 (4.11)</td>
<td>12.13 (4.88)</td>
<td></td>
</tr>
<tr>
<td>Composite</td>
<td>39</td>
<td>0.321</td>
<td>10.96 (2.29)</td>
<td>13.88 (2.71)</td>
<td></td>
</tr>
</tbody>
</table>

---

**TABLE 4**—Leaf area analysis results for Evan Jones Mine collections of the upper Chickaloon Formation. MAP = mean annual precipitation. See text for further explanation.

<table>
<thead>
<tr>
<th>Collection</th>
<th>MinA</th>
<th>MAP (cm)</th>
<th>Std. error low</th>
<th>Std. error high</th>
</tr>
</thead>
<tbody>
<tr>
<td>C (n = 21)</td>
<td>7.85</td>
<td>158.9</td>
<td>110.9</td>
<td>227.5</td>
</tr>
<tr>
<td>B (n = 22)</td>
<td>8.57</td>
<td>160.3</td>
<td>111.9</td>
<td>229.5</td>
</tr>
<tr>
<td>Composite (n = 39)</td>
<td>7.6</td>
<td>154.6</td>
<td>107.9</td>
<td>221.4</td>
</tr>
</tbody>
</table>

**Leaf Damage**

---

**TABLE 3**—CLAMP results for the Evan Jones Mine leaf collections and the composite Chickaloon paleoflora analyzed in Wolfe (1994). MAT = mean annual temperature, WMMT = warm month mean temperature, CMMT = cold month mean temperature, GROWSEAS = growing season (months), GSP = growing season precipitation, 3WET = precipitation during three wettest months, 3DRY = precipitation during three driest months.

<table>
<thead>
<tr>
<th>Parameter (st. dev.)</th>
<th>B (n = 22)</th>
<th>C (n = 21)</th>
<th>Composite (n = 39)</th>
<th>Wolfe (1994) (n = 29)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAT (°C) (1.17)</td>
<td>13.5</td>
<td>13</td>
<td>13.7</td>
<td>12.3</td>
</tr>
<tr>
<td>WMMT (°C) (1.58)</td>
<td>22.3</td>
<td>21.7</td>
<td>22.2</td>
<td>23.5</td>
</tr>
<tr>
<td>CMMT (°C) (1.88)</td>
<td>5.6</td>
<td>5.3</td>
<td>6.1</td>
<td>6.1</td>
</tr>
<tr>
<td>GROWSEAS (33.59)</td>
<td>114.3</td>
<td>122.9</td>
<td>118</td>
<td>&gt;145</td>
</tr>
<tr>
<td>3WET (cm) (14.03)</td>
<td>63.4</td>
<td>66</td>
<td>63.5</td>
<td>not reported</td>
</tr>
<tr>
<td>3DRY (cm) (9.30)</td>
<td>39.9</td>
<td>39.3</td>
<td>36.6</td>
<td>not reported</td>
</tr>
</tbody>
</table>
Trop et al. (2003) interpreted sedimentary structures elsewhere in the Chickaloon Formation as tidally influenced. We feel this constraint in depositional elevation eliminates the possibility that the leaf-climate indicators are recording anomalous climate conditions due to high elevation. This observation does not rule out regional land-sea climate amelioration (sea breezes, for example) and orographic climatic influences in the basin, however.

LMA, PLMA, and CLAMP yield a range of MAT estimates (11.3 °C for LMA in Bed C, to 14.6 °C for PLMA in Bed B) with little significant variation between collections and large standard deviations across beds with presumed rapid sedimentation (Flores and Stricker, 1993; J. Neff, personal communication, 2011). Because fossiliferous beds of the upper Chickaloon document the presence of presumed hydrophilic flora and fauna as well as fluvial sedimentary structures indicative of meandering stream settings, the Kowalski and Dilcher (2003) PLMA regression may be most appropriate for this study. This puts our best estimate of MAT in the upper Chickaloon Formation between 13.8 °C and 14.6 °C.

Whichever MAT estimation methods are employed, the results imply a climate that was warmer than today (~1.5–3 °C MAT currently at Sutton, Alaska), but cooler than expected for rocks of this age in Alaska when compared with the conclusions of Wolfe et al. (1966). These authors suggested that the entire flora of the Chickaloon Formation represented subtropical conditions due to the presence of tropical leaf taxa such as fan palms (Sabalites) and the euphorb Macaranga. They also reported that nearly half of a composite assemblage from the formation had entire margins, suggesting temperatures >18 °C (using the Wilf (1997) LMA equation). Our upper Chickaloon collections lack the tropical taxa found in Wolfe et al.’s (1966) composite collection, however, and our analyses indicate considerably cooler temperatures in the uppermost fossiliferous beds of the unit. Our data corroborate Wolfe’s (1994) CLAMP analysis of a composite collection of 29 morphospecies from the Chickaloon Formation which yielded an MAT estimate of 12.3 °C (Table 3). In slightly younger strata of the Kulthieth Formation, Wolfe (1977) describes the early Ravenian (early?–middle Eocene) of southern Alaska as paratropical with MAT ranging from 20 to 25 °C (65% entire margined). CLAMP analysis of this same flora (Wolfe, 1994) indicated an MAT of 19.4 °C. We do not recognize such a climate signal in our Chickaloon data, nor do we see evidence for a strong climate warming spike similar to those that represent the PETM elsewhere (Wing et al., 2005). Our relatively low temperature estimates are consistent through and across the Evan Jones Mine exposure and do not vary considerably with the samples we have near (but not on) a heretofore unexplained strong negative carbon-isotope excursion (J. Neff, personal communication, 2011).

**FIGURE 5**—Leaf damage examples in the upper Chickaloon Formation. A) Hole feeding with reaction tissue (*Magnolia magnifolia*?). Note reaction tissue (darker area around hole). B) Skeletonization damage (*Zizyphoides flabella*). C) Surface-feeding damage with reaction tissue (“Sinowilsonia” sp.). D) Margin feeding (*Haemanthophyllum* sp.). All scales = 1 cm × 0.5 cm.
If a climate anomaly at the PETM is recorded in the sequence, we believe that the sampled beds in this study lie >10 m above any such signal based on proximity to the now-buried Premier Coal Zone (Fig. 3) and the Paleocene–Eocene boundary (Triplehorn et al., 1984). Wing (1998) and Fricke and Wing (2004) found that in the Bighorn Basin about 1.5 myr after the end of the PETM, temperatures dropped from >18°C MAT to ~11°C in the upper Haplonylvius-Ectocion Zone (UHEZ) before rising again. The warm temperate conditions reported herein may correspond in time to these low temperatures of the UHEZ. Further geochronological work on the upper Chickaloon Formation will clarify these age relationships.

The absence of a well-supported paleolatitude of deposition for the Chickaloon Formation makes it difficult to put the climatic results from this study into a paleogeographic context. While Stamatakis et al. (1989) provide paleomagnetic data which places the Matanuska Valley–Talkeetna Mountains forearc basin at 48° N ± 11° during the late Paleocene–early Eocene, Wolfe (1994) suggests that Chickaloon deposition may have occurred as high as 76° N because of its terrane connection with data in Hillhouse and Gromme (1982). Still other analyses (Hillhouse et al., 1985; Panuska et al., 1990) suggest that the basin has experienced no offset since 55 Ma. Fricke and Wing (2004) estimate a paleoclimatic gradient for North America in the early-middle Eocene. Although there is a large data gap between 50° and 80° N due to, and resulting in, uncertainty at these latitudes, extrapolation of predominantly mid-latitude regression curves derived from coastal–low elevation and large basin sites similar to the depositional setting of the Chickaloon Formation results in a mean annual temperature estimate of 12–15°C. This corresponds to about 60° N, near the northern end of the possible ranges of paleolatitude as determined by Stamatakis et al. (1989), and matches with our leaf-estimated MAT. This extrapolation suggests that the Matanuska Valley–Talkeetna Mountains basin may have been very close to its present latitude during the deposition of the upper Chickaloon. If, however, the paleolatitude of deposition of the upper Chickaloon was near 48° N, the regressions hindcast an MAT of 17–22°C. This value is higher than our estimates, but within our margin of error. The regression predicted an MAT of 25°C for 37° N, the southern end of the published range of possible paleolatitudes for the Chickaloon, which is inconsistent with any of our analyses.

Although investigations into plant-insect associations near the Paleocene–Eocene boundary in North America have been fruitful at mid-latitude sites (e.g., Curran et al., 2008), until now no analyses have been performed at northern polar to subpolar paleolatitudes. Hole-feeding, margin-feeding, skeletonization, and surface-feeding types are preserved in the Chickaloon collection, leaving only galling and leaf mining as the major damage guilds not observed in the collection. The damage character and diversity of feeding guilds in the Chickaloon is not significantly different than that noted in floras of similar age elsewhere in North America (e.g., Smith, 2008; although see Labandeira, 2002). Where the Chickaloon seems unique, though, is in the relative paucity of damage when considering the number of undamaged versus damaged leaves and leaf fragments in the collection. Although extensive studies of Paleocene–Eocene leaf damage from Bighorn Basin collections (Wilk and Labandeira, 1999, 2000; Wilf et al., 2001; Curran et al., 2008) include many analyses not yet possible with existing Chickaloon collections, we can compare Smith’s (2008) published damage frequency data with our existing collections.

Only 9.4% (63 of 669) of the leaves and leaf fragments from Chickaloon Beds A–E that were considered for herbivory exhibit some sort of damage; of those damaged leaves, 19% were damaged in more than one fashion. This overall damage incidence is notably lower than that of Smith’s (2008) middle Eocene Green River and late Eocene Florissant collections (34% and 23%, respectively), data that were gathered and analyzed in the same fashion. The percentage of total leaf area damaged was also low in the Chickaloon Formation (0.48%) as compared to Smith’s (2008) data from Colorado (Table 5). Direct comparison with Curran et al.’s (2008) Bighorn Basin insect damage data is not yet possible because that study’s sampling protocol considers specimens only if at least half of the leaf is preserved. Even so, we believe that future Chickaloon flora leaf-damage sampling by this method is unlikely to rival the reported high damage frequency at the P-E boundary (57.3%) and within the early Eocene (Wasatchian 2) (33.3%) in the Bighorn Basin (Curran et al., 2008).

This frequency of herbivory has been shown to be positively correlated with temperature in both the recent (Coley, 1998, 1999) and the fossil record (Wilk and Labandeira, 1999; Wilf et al., 2001; Smith, 2008; Wilf, 2008). Elevated temperatures generally result in higher metabolic rates for herbivores and therefore greater leaf herbivory potential at lower latitudes (Brown et al., 2004), where insects theoretically reach feeding maturity more quickly and with greater regularity throughout the year (Coley and Aide, 1991). Curran et al. (2008) noted that increases in the frequency and diversity of insect damage reflect rising temperatures in Wyoming from the Paleocene into the earliest Eocene (including the PETM). It would seem likely that the significantly lower frequency of herbivory in the Chickaloon would reflect lower temperatures as well. Our estimated upper Chickaloon MAT of ~13–14.5°C, however, is not greatly different from the MAT estimates of the Bighorn succession (Curran et al., 2008), nor is it significantly lower than the Green River and Florissant collections with much higher damage frequencies (Smith, 2008) (Table 5).

Our MAP estimates for the Chickaloon indicate wet conditions, both as compared to the present and to the comparison sites studied for herbivory elsewhere in North America (Smith, 2008). Herbivory frequency is positively correlated with precipitation (Wilk et al., 2001). Moisture availability is also essential for leaf growth and thus decreased moisture is associated with decreased leaf size and increased leaf thickness (Givnish, 1987), characteristics that make leaves less appealing to herbivores. An abundance of precipitation and other environmental conditions results in short-lived leaves with high nutritional value leading to overall higher rates of herbivory (Wilk et al., 2001). The Chickaloon samples yielded much higher MAP estimates than both the Green River and Florissant Formations (Smith, 2008) (Table 5) and the Chickaloon damage frequency is therefore unexpectedly low for this reason as well.

Our data suggest that neither MAT nor MAP seem to be a strong determinant of herbivory frequency at the time and place of Chickaloon deposition. Indeed our findings are counter to expectations concerning both of these factors. Complicating factors, including seasonal-to-
decadal variability in climate, timing of leaf maturity relative to insect life history, and local depositional environment stability may contribute to these observations (Coley, 1980, 1987; Coley and Barone, 1996). If a latitudinal gradient in the diversity of Eocene insects mirrored the pattern we observe in the recent, low damage frequency at high latitudes may be attributable to fewer folivorous insect taxa at high latitudes (but see Archibald et al., 2010). Additionally, our data suggest that the modern latitudinal gradient in damage frequency includes a significant contribution from the greater extremes in seasonality (including the light regime) at high latitudes. We lack a modern analogue for warm, seasonally averaged conditions at high latitudes that would aid in recognizing the importance of these factors. The fact that we recovered only moderate leaf diversity (n = 39) in our samples from the upper Chickaloon, as compared to comparison assemblages, may also contribute to the low incidence of herbivore damage, especially since many datasets have supported the hypothesis that plant and insect diversity are correlated in modern ecosystems (e.g., Murdoch et al., 1972).

Although no arthropod impressions have been discovered in the Chickaloon, dispersed aril found within coaly lithofacies at the base of the Evan Jones Mine section preserves a modest insect diversity, some of which may be responsible for the noted herbivory. If this association can be supported with further collection and analysis, the locality would be unique in possessing the fossil remains of both the potential herbivores in an amber fauna and their possible feeding traces on fossil foliage compressions.

CONCLUSIONS

Upper strata of the late Paleocene-early Eocene Chickaloon Formation in south-central Alaska preserve a fluvial depositional environment with a diverse and well-preserved assemblage of fossil dicot leaves, some of which show evidence of insect damage. Estimates of mean annual temperature (using LMA, PLMA, and CLAMP methods) from earliest Eocene leaf fossil assemblages in the upper Chickaloon Formation at the Evan Jones Mine indicate warm-temperate conditions (−11–14.6 °C ± −3 °C MAT). Large standard deviations and rapid, laterally heterogeneous depositional rates, however, make it difficult to discern if small-scale climate change is represented in the studied section. The temperature-latitude regression from the early Eocene shows that the mean annual temperature reported in this study is consistent with a paleolatitude close to present (62 °N) during the deposition of the Chickaloon Formation.

This work also constitutes the first study of plant-insect interactions in a high paleolatitude assemblage. About 9% of leaf and leaf-fragment specimens showed at least one type of plant-insect interaction, a frequency lower than expected considering the damage frequencies in lower latitude Eocene North American assemblages under similar or only slightly higher paleotemperatures. As latitudinal variation in plant-insect associations has been observed in modern ecosystems (Coley and Aide, 1991; Coley and Barone, 1996), more data from Paleocene–Eocene high-latitude assemblages such as the Chickaloon will help in investigating these paleoecological interactions in non-analog climate and light-regime conditions.

ACKNOWLEDGMENTS

We acknowledge field and analytical support from D. Merkert, J. Neff, K. Trostle, B. Walker, L. Stout, D. Hubbard, and the state of Alaska. Funding was provided by the Keck Geology Consortium, Lafayette College, and Franklin & Marshall College. This manuscript was improved by thoughtful reviews from E. Curran, D. Smith, and E.L. Taylor.

REFERENCES


Heard, O., 1869, Contributions to the fossil flora of North Greenland, being a description of the plants collected by Mr. Edward Whymper during the summer of 1867: Philosophical Transactions of the Royal Society of London, v. 159, p. 445–488.


SUNDERLIN ET AL.


Accepted March 9, 2011