PALEOCLIMATE OF THE TWO MEDICINE FORMATION

BASED ON LEAF PHYSIOGNOMY

by

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ILLUSTRATIONS

Illustration	Page

LIST OF ABBREVIATIONS

Abbreviation   **Description**

MAT— Mean Annual Temperature

LMA— Leaf Margin Analysis

MAP— Mean Annual Precipitation

 LSI— Leaf Size Index

CMMT— Cold Month Mean Temperature

LAA— Leaf Area Analysis

CLAMP— Climate Leaf Analysis Multivariate Program

WMMT— Warm Month Mean Temperature

GSP— Growing Season Precipitation

DiLP— Digital Leaf Physiognomy

FDR— Feret Diameter Ratio

PR— Perimeter Ratio

IP— Internal Perimeter

MART— Mean Annual Range of Temperture

ABSTRACT

Over the past 50 years, methods to study ancient warm climates, like those of the Cretaceous, have yielded new information on climates and their interaction with flora and fauna. One of the effective ways to reconstruct paleoclimates in terrestrial environments is the study of external features of leaves, or foliar physiognomy. Features of leaves from different climates have been correlated to mean annual temperature (MAT), mean annual precipitation (MAP), and other climate variables. There are several methods to determine paleoclimate based on the modern-day correlation between leaf features and climate parameters. These methods include the univariate methods of leaf margin analysis (LMA) and leaf area analysis (LAA), and the multivariate methods of Climate Leaf Analysis Multivariate Program (CLAMP) and Digital Leaf Physiognomy (DiLP). This study uses these paleoclimate proxies to study the Two Medicine Formation, a famous formation in northern Montana that contains both dinosaur and paleobotanical remains. In addition, the research examines the congruence of different physiognomic methods with each other and with other climate proxies for the Two Medicine Formation and surrounding formations of similar age. This study concludes that the univariate methods give temperature estimates that are too low, and the multivariate methods give precipitation estimates that are too high. Of the two multivariate methods, CLAMP gives slightly lower temperature estimates and has inconsistencies based on classification of leaf features, but is still able to provide seasonality signals. DiLP, on the other hand, gives more reasonable estimates for MAT based on congruence with other paleoclimate

proxies. However, the DiLP image processing of the leaves is more complex and time

consuming than that of the other methods. In order to cut the leaf image processing time,

a new modified technique of *doubling the leaf halves* from partial fossil specimens was

implemented in this study. Preliminary results from the doubling halves technique

indicates that climate parameter estimates are nearly the same as those described in the

original DiLP method.

I. INTRODUCTION

Background and Rationale of the Study

Dinosaurs are creatures that have captivated humanity since the discovery of the first fossils, and sparked many research expeditions to find, collect and understand them. These magnificent creatures once inhabited the current western United States before the Alvarez asteroid impacted the Yucatan Peninsula, Mexico, which either caused or helped further their extinction (Gates et al., 2012; Alvarez et al., 1980; Schulte et al., 2010). One rock formation from Montana, the Two Medicine Formation, has yielded several significant dinosaur skeletons, including Ceratopsids, Hadrosaurids, and Ankylosaurids (Rogers, 1990; Penkalski, 2014; Crabtree, 1987b; Rogers, 1990; Falcon-Lang, 2003). In recent years, research has focused on the ecology and environment that these dinosaurs lived in when the formation was being deposited (Chin and Gill, 1996; Chin, 2007; Retallack, 1997; Rogers, 1990).

One of the most important factors that affects any environment is climate. The past climate, or paleoclimate, is estimated from proxies, stand-in factors that are directly affected and measured from the different parameters of the climate. Different proxies, and the subsequent climate readings from them, can be used to create and test models that predict temperatures during warming climates, particularly during ancient geologic times when high atmospheric CO_2 gas levels were more common (Beerling et al., 2002; Upchurch et al., 2007; Lomax et al., 2000; Linnert et al., 2014).

It is a long recognized fact that plants are directly influenced by the climate that they grow in. Bailey and Sinnot (1915, 1916) proposed a correlation between the percentage of leaves with entire (untoothed) margins and warm climates, by qualitatively comparing tropical and temperate floras globally. Warm climates will usually contain a higher portion of entire margined species, while cooler, temperate climates will have a higher portion of toothed species (Bailey and Sinnot, 1915, 1916). In the 1970s, Jack Wolfe (e.g., Wolfe, 1979) expanded upon the 1916 work by including other East Asian floras and graphing mean annual temperature (MAT) versus percentage of entire-margined species in a plant community. The resulting correlation showed a linear rise in temperature with increasing percent entire, which quantitatively confirmed the observations of Bailey and Sinnot (1916). This method, now called leaf margin analysis (LMA), has been the founding work for many current climate estimates through botanical methods.

By studying the leaf margins and other leaf characteristics, the relationship between leaf physiognomy and climate can be further refined (Bailey and Sinnott, 1915; Huff et al., 2003; Peppe et al., 2011; Greenwood, 2007; Wilf et al., 1998; Traiser et al., 2005). Having determined the correlation between leaf characteristics and temperatures in modern floras, fossil floras can be used establish paleoclimate estimates. Physical characteristics found in modern leaves, can be seen on fossil leaves (i.e. Law of Uniformitarianism: what is happening/seen today, can happen/be seen in the past), which can be subsequently used as paleontological proxies for other fields e.g., Upchurch and Wolfe (1987) and Upchurch et al. (2015). These modern floras, and their adjacent metrological stations/data, are the basis for all the methods discussed in this study.

This study examines the paleoclimate of Late Cretaceous, focusing on the Campanian stage (83–72 Ma) Two Medicine Formation of Montana. One preliminary paleoclimate analysis was done as part of a University of Montana doctoral dissertation (Crabtree, 1987a, 1987b). Over the subsequent three decades, several new botanical climatic proxy methods have been developed (Wolfe, 1993; Huff et al., 2003; Royer et al., 2005; Wilf et al., 1998; Peppe et al., 2011). These new methods are utilized to update previous MAT estimates and to establish preliminary estimates for mean annual precipitation (MAP) for the Two Medicine Formation.

Geologic Setting of the Two Medicine Formation

During the deposition of the lower Two Medicine Formation, the world looked very different from that of today (Kaufmann and Caldwell, 1993; Rogers et al., 1993; Blakey, 2014; Miall and Blakey, 2008; Crabtree, 1987b). The Campanian stage is characterized by the Atlantic Rift separating the North American and the Eurasian continents (Figure 1) (Miall and Blakey, 2008; Kauffman and Caldwell, 1993). On the North American continent, the Western Cordillera was a series of accreted volcanic island arcs that were carried on the subducting Farallon Plate and comprised the western edge of the continent (e.g., Miall and Blakey, 2008; Kauffman and Caldwell, 1993). This subduction led to several magmatic craton and pluton episodes that extended in a north to south trend characterized by the many ash beds found in basins of the Cordillera (Monger, 1993; Kauffman and Caldwell, 1993). These volcanic island arcs began to uplift and be folded during the Sevier Orogeny. They rose further by basement
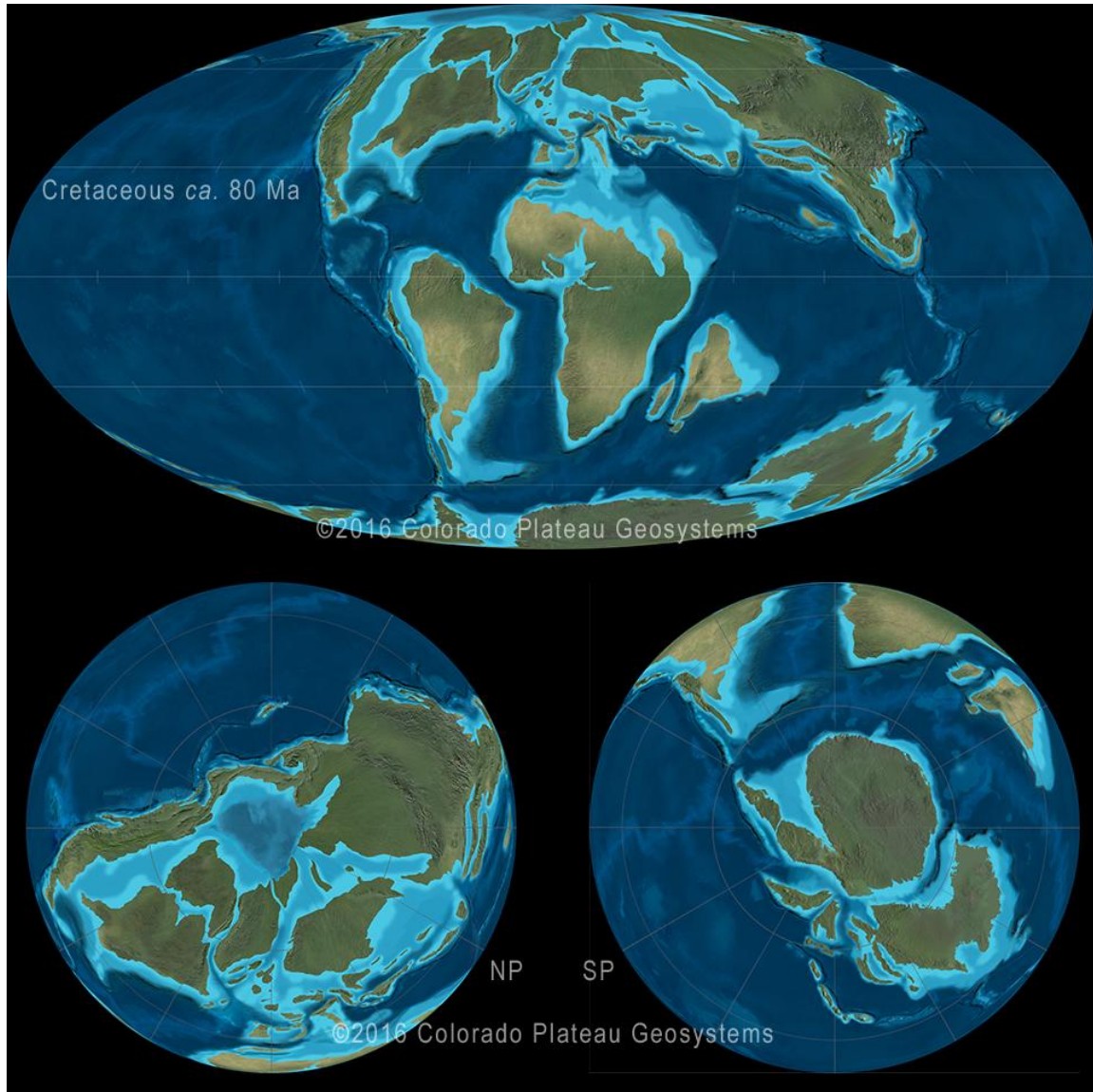
Figure 1. The global configuration of the Earth at 80 million years ago as taken from the data of Ron Blakey (2014). This figure shows the North American continent being separated into two landmasses: an eastern Appalachia and a western Laramidia (Gates et al., 2012; Kauffman and Caldwell, 1993; Crabtree, 1987b; Blakey, 2014; http://deeptimemaps.com/wp-content/uploads/2016/05/080_Ma_Late-Cret_GPT-1.png).

central uplifting that caused fault blocking during the Laramide Orogeny, leading to the current Rocky Mountain range (Armstrong and Ward, 1993; Kauffman and Caldwell, 1993; Crabtree, 1987b; Miall and Blakey, 2008; Miall et al., 2008).

Due to the crustal loading on the west coast from the uplifted accreted volcanic arcs, there was a thinning and down-warping of the crust directly east of these mountains, causing a basin to form in the middle of the continent that filled with saline water (Kauffman and Caldwell, 1993; Miall et al., 2008). The water-filled basin, called the Western Interior Seaway, extended from Mexico and Texas to the Northwestern territories of Canada and Arctic Ocean. This seaway left many characteristic transgressive and regressive sequences and broke the continent into two halves; an eastern Appalachia and a western Laramidia (Figure 2) (Gates et al., 2012; Kauffman and Caldwell, 1993; Crabtree, 1987a). During the Late Campanian or Maastrichtian, this seaway began to shallow and drain as the basement rock uplift of the Laramide Orogeny increased (Miall et al., 2008).

The rock formation of interest is the Two Medicine Formation near Cut Bank Creek, Montana, USA. Stratigraphically, the Two Medicine Formation includes layers of non-marine shale, sandstone, and bentonite (volcanic ash altered to clay) deposited in fluvial or floodplain environments. Because of the presence of bentonite, unoxidized sediments, and fresh water gastropods, Crabtree (1987b) hypothesized that there may have been consistent fresh water for the majority of the time. These sediments originated from the Cordilleran highlands and the ancient Elk Horn Mountain Volcanoes to the west and southwest respectively (Figure 2) (Crabtree, 1987b; Rogers et al., 1993). The Two Medicine Formation grades into the shoreline faces of the Judith River Formation after

Figure 2. The configuration of the Western Interior Basin at 80 million years ago. Image taken from the data of Ron Blakey (2014) and modified to include the Crabtree (1987b) fossil leaf locality as indicated by the blue star (Kaufmann and Caldwell, 1993; Rogers et al., 1993; Blakey, 2014; http://deeptimemaps.com/wp-content/uploads/2016/05/wiscretcam6.png).
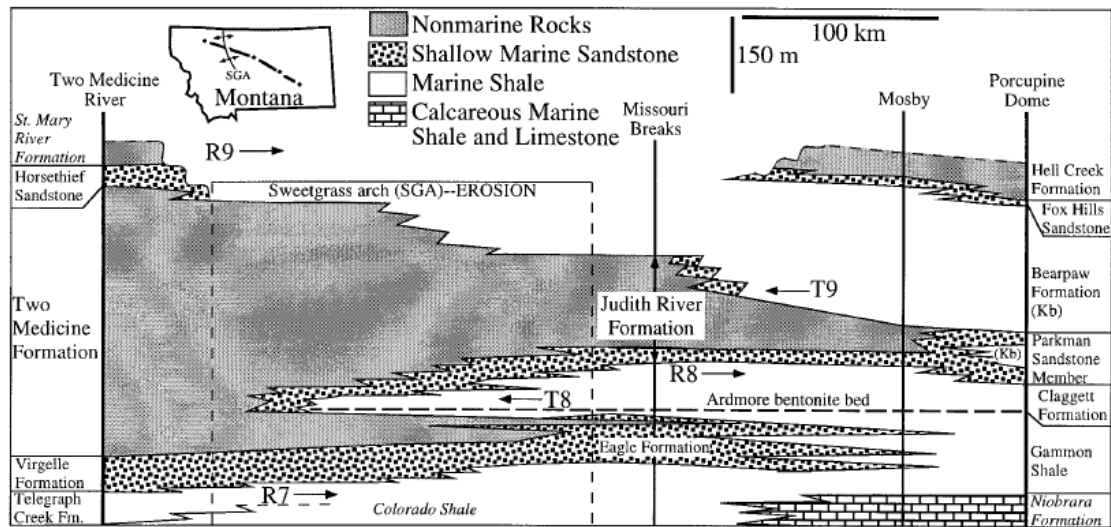
Figure 3. Schematic cross section of the study area, taken from the work of Rogers (1998). It shows the gradational distance from the inland Two Medicine Formation to the coastal Judith River Formation at the Sweetgrass Arch. This distance is estimated to be 150 to 320 km.

Figure 4 A. Stratigraphic columns presented in Crabtree (1987b), where the United States named formations change at the Canadian border. The corresponding formations must be coeval to the depth and age of Crabtree's (1987b) fossil leaves, if indicator fossils are described. **B.** Updated coeval stratigraphic columns that span the Western Interior Basin. The blue star indicates level of fossils (Gates et al., 2010).

the Sweetgrass Arch (Figure 3) (Rogers, 1998), and changes names to the Milk River, Pakowki, and Foremost formations at the US/Canadian border to (Figure 4) (Crabtree, 1987b).

The lower part of the Two Medicine Formation, which contains the leaf fossils examined in this study, is dated at ~ 79.60 ± 0.1 Ma based on $^{40}Ar/^{39}Ar$ from volcanic ashes in a stratigraphic section less than 20 km from the fossil description site (Figure 5) (Foreman et al., 2008; Crabtree, 1987b). This dates the lower Two Medicine Formation as middle Campanian stage of the Upper Cretaceous (Cohen et al., 2018;Gates et al.,2010). Paleogeographically, the Two Medicine Formation was located 150 to 320 km inland from the western shoreline (Laramidia) of the Western Interior Seaway at ~54° N paleolatitude (Figure 2, Figure 3, and Figure 6) (Van Hinsbergen et al., 2015; Gates et al., 2012; Kauffman and Caldwell, 1993; Crabtree, 1987b; Blakey, 2014; Rogers et al., 1993; Rogers, 1998; Roberts and Hendrix, 2000; Falcon-Lang, 2003; Miller et al., 2013; Prue et al., 2015). Miller et al. (2013) extends the Two Medicine to 56°N paleolatitude. The entire formation is ~ 600 m thick with an exposed north-south expanse of ~250 km and ~50 km wide (Falcon-Lang, 2003; Crabtree, 1987a, 1987b).

The analyzed fossils are non-monocot woody flowering plant (dicot) leaves that were collected at SE ¼, Sec. 18, T. 32 N, R 5 W (48.57 Latitude, -112.18 Longitude) along the channel escarpment of Cut Bank Creek, at about 6 km south of the town of Cut Bank, Montana in Glacier County (Figure 5) (Crabtree, 1987b; Rogers et al., 1993). These fossils occur ~ 20 m above the base of the formation in two horizons separated by 0.5 m (Crabtree, 1987a, 1987b) and were collected and described by David R. Crabtree (1987b) for his PhD thesis. He described twenty-eight fossilized dicot leaf morphotypes

(≈ species) that are distinguishable by venation and shape. While most of his thesis describes leaf morphotypes, he analyzed the leaves for preliminary paleoclimate interpretations that followed Wolfe and Upchurch's (1987) LMA calibration (Crabtree, 1987b). Using these features, Crabtree (1987b) inferred that the MAT was 7-10°C, without an extended cold season due to the presence of palms. This temperature range, he noted, is similar to that of other fossil localities in the region but is anomalous for the time period of similar paleolatitudes (Crabtree, 1987b). Crabtree (1987b) also analyzed leaf size using leaf size index (LSI), which uses the percentage of species with different leaf sizes to calculate an average leaf size (Wolfe and Upchurch, 1987). Leaf size gets smaller in response to decreasing temperature and water availability, and/or increasing light. Therefore, relative leaf size provides an indication of the paleoclimate (Upchurch and Wolfe, 1987; Wilf et al., 1998). Crabtree's (1987b) LSI calculations give a very generalized climate description of megathermal (tropical) climate with possible wet-dry seasonality for the Two Medicine Formation. However, this LSI method was not comprehensibly studied. This climate estimate is contradicted by LMA, which suggests MAT of 7-10°C, a characteristic of colder climate regimes (i.e., temperate deciduous forest and costal conifer forest). The LSI method suggests tropical temperatures of megathermal climates (Wolfe and Upchurch, 1987; Crabtree, 1987b). Crabtree (1987b) notes this contradiction in his thesis, and uses the combined information from LMA, LSI, and the deciduous dicot of leaves found to conclude that the Two Medicine is a successional mesothermal deciduous forest, a climate regime proposed by Wolfe and Upchurch for early Paleocene forests (1986).
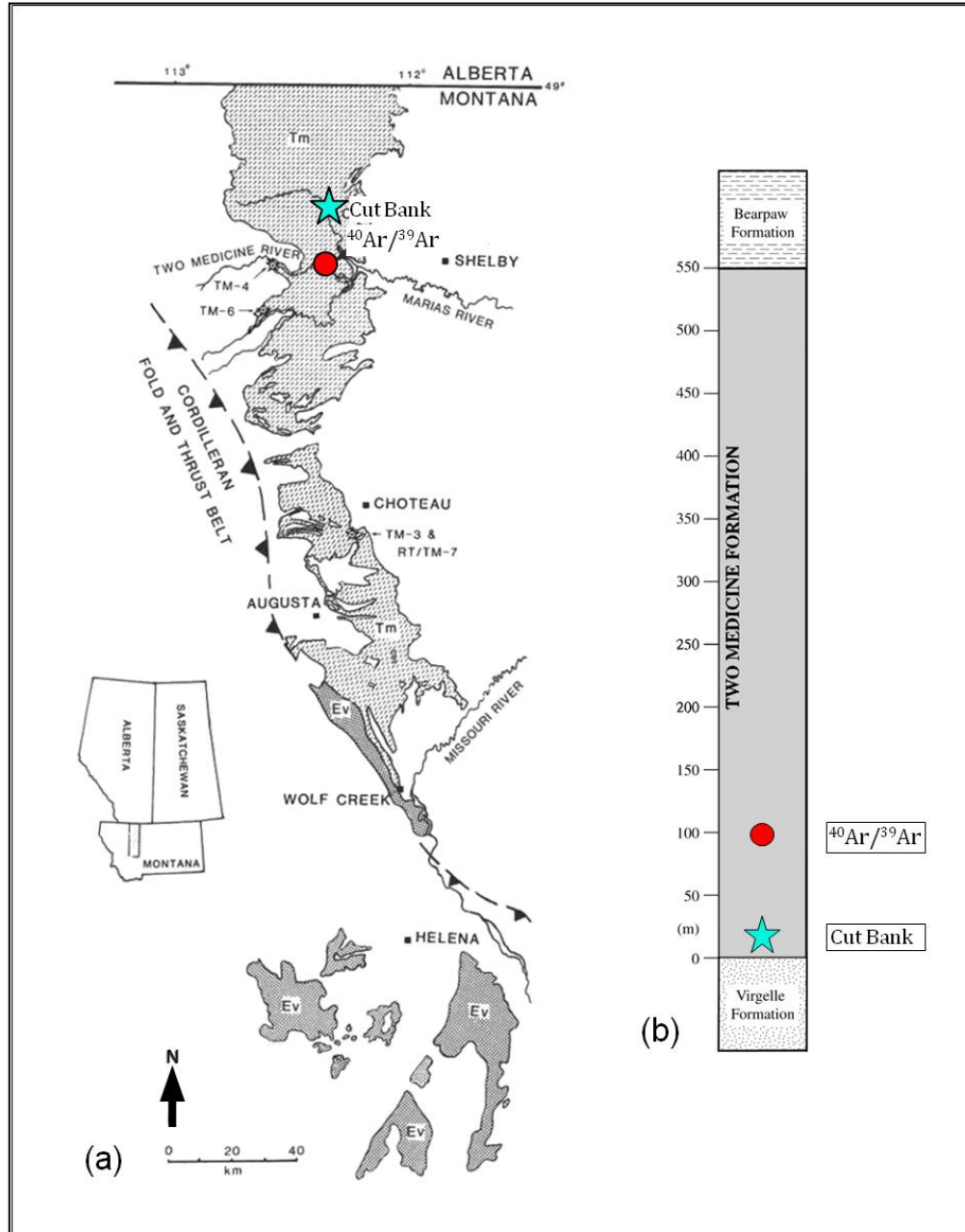
Figure 5. Geologic map and a simple stratigraphic column of the Two Medicine Formation. The blue star is the approximate location of Crabtree's fossil locality (1987), while the red circle is the location of the $^{40}Ar/^{39}Ar$ dating sample. The age estimation is ~79.6 Ma. **a.** Modified from the work of Rogers et al. (1993), **b.** Modified from the work of Foreman et al. (2008). This image and caption were presented in Prue, Upchurch, and Chin, (2015).
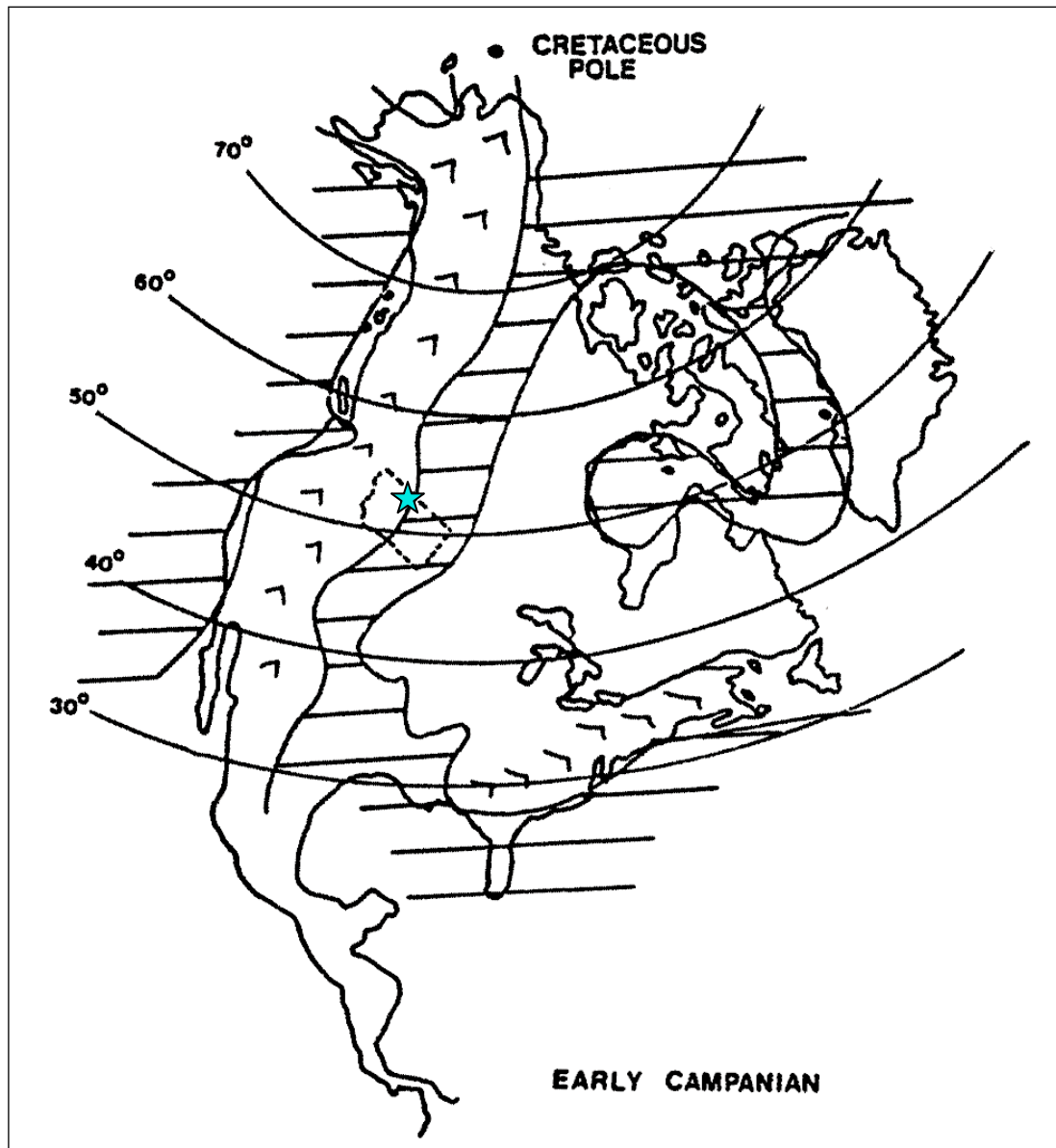
Figure 6. Simplified paleogeographic reconstruction of North America during the middle Campanian, with the location of Montana and the Two Medicine Formation (dashed lines). The blue star is the approximate location of the fossil leaf beds. Montana was located at ~54° N paleolatitude (Van Hinsbergen et al., 2015). Map modified from the work Crabtree (1987b) and Prue et al., (2015).

Paleoclimatic Patterns of the Western Interior

Paleoclimate studies for the Western Interior Basin are based on animal and plant fossils and oxygen isotopes. Miller et al. (2013) gives a comprehensive overview of the paleoclimatic trends and patterns of the Campanian Western Interior, while Wolfe and Upchurch (1987) and Upchurch and Wolfe (1993) place the Western Interior within the context of North America. Sea surface temperatures during the late Campanian and Maastrichtian Western Interior Seaway are estimated to have been 25-35+˚C based on stable $\delta^{18}O$ and Δ_{47} clumped isotopes (Miller et al., 2013; Dennis et al., 2013; Upchurch et al., 2015). Estimated seaway temperatures have been compared to the adjacent terrestrial regions via paleobotany (i.e. LMA) (Miller et al., 2013). The issue with isotopic values is that they can be compromised by terrestrial input, freshwater input, salinity modifications, and/or diagenetic alteration (e.g., Upchurch et al., 2015). Miller et al. (2013) examined at thirty previously described megafloras, including the Two Medicine Formation (though no great detail was mentioned), that span the western margin of the Western Interior Seaway. Working off the idea of the work in Wolfe and Upchurch (1987), these megaflora's paleotemperatures show a paleolatitudinal gradient of 0.4˚C/˚N MAT and no freezing temperatures until 80˚N (Miller et al., 2013; Upchurch et al., 2015).

Precipitation estimates are complex and difficult to determine with accuracy. Wolfe and Upchurch (1987) presented a preliminary distribution of precipitation for North America that includes Western Interior Basin, which was updated by Miller et al. (2013). The precipitation of the region can be broken down into three bands. Below 50˚N

there is much less rainfall when compared to the paleolatitudes of 50-60°N. Latitudes above 50°N are hypothesized to have high rainfall (Miller et al., 2013). This transition is also indicated by a decrease in leaf size between similar age fossil floras. However, when analyzing southern floras from the Western Interior, the relation between rainfall and leaf size becomes more complex (Miller et al., 2013; Wolfe and Upchurch, 1987; Upchurch and co-workers, work in progress). The third band covers the region above 60°N, where it is described as being moderate to high rainfall (Miller et al., 2013). Miller et al. (2013) noted that there could be monsoonal precipitation patterns in this band, which could affect botanical seasonality indicators. Wolfe and Upchurch (1987) make note of wood samples, with a paleolatitude of 63°N, that show annual rings, that would be indicative of seasonality, but false annual rings (e.g. caused by herbivory) are also present. Their hypothesis is that there was varied precipitation at the end of each growing season (Wolfe and Upchurch, 1987). In contrast to the higher paleolatitudes, the lower paleolatitudes can show drier conditions based on paleosols, as for instance indicated by New Mexico's Crevasse Canyon Formation (Mack, 1992). From the lack of caliche in the paleosols, the climate of the middle Campanian was described as humid to sub-humid with 60+ cm/yr precipitation estimates (Mack, 1992). Using this combined information, the precipitation decreases moving from north to south along the Western Interior Basin.

One goal of this study is to more accurately reconstruct climate for the lower Two Medicine Formation. As stated previously, David R. Crabtree (1987b) used leaf physiognomy to infer the climate of the Two Medicine Formation at Cut Bank Creek,

Montana. He described twenty-eight dicot morphotypes characterized by separate

distinguishable architectural features (i.e. veins and leaf shape) that can be used to

estimate the paleoclimate.

II. REVIEW OF LITERATURE

Paleoclimate and Methods

Physical characteristics of leaves that are useful for climatic reconstruction include leaf margin type, tooth number and size, and leaf area. The presence of an entire, or untoothed margin, has been correlated with MAT (e.g., Wolfe, 1971, 1979; Upchurch and Wolfe, 1987; Peppe et al., 2011, Huff et al.,2003; Royer et al., 2005; Wilf, 1997; Uhl and Mosbrugger, 1999). Teeth are described as extensions of vascular tissue that extends less than a quarter of the distance to the mid-vein; with greater distance, leaves are considered lobed (Royer et al., 2005; Ellis et al., 2009; Oliver, 2010; Royer and Wilf, 2006). The presence of teeth is an important consideration because more toothed species, larger tooth areas, greater number of teeth, and greater dissection of leaves are found in colder climates (Royer et al., 2005; Peppe et al., 2011; Huff et al., 2003; Royer and Wilf, 2006). Leaf area is described as all parts of the blade and provides information on humidity and precipitation amounts (Huff et al., 2003; Royer et al., 2005; Royer, 2012; Upchurch and Wolfe, 1987; Wilf et al., 1998; Oliver, 2010; Peppe et al., 2011). These features, the leaf physiognomy and leaf economic variables, are a proxy for climate because they are influenced by the temperature in the atmosphere, water availability, and mineral nutrient uptake (Royer et al., 2005).

Two univariate methods used by Crabtree (1987b) are LMA and LSI. LMA is derived from the correlation between the proportion of entire margined leaves of flowering woody plants in a flora and MAT. This analysis requires a minimum of twenty distinct species/morphotypes (e.g., Royer et al., 2005). Wolfe (1979, 1993) analyzed

extant eastern Asian dicot species and determined that there is roughly a 3% increase in the percentage of entire margined species per degree Celsius mean annual temperature. This calibration, seen in Table 1, can be used to infer paleo-MAT using the percentage of dicot species with entire versus toothed margins (Wolfe, 1993). Wolfe's (1979, 1993) calibration has since been reevaluated and updated using floras from the Northern and Southern Hemispheres (Table 1) (Peppe et al., 2011; Wilf, 1997; Greenwood et al., 2004; Miller et al., 2006).

Using Wolfe's (1979) LMA, Crabtree (1987b) inferred that the climate of the Two Medicine Formation had a MAT range of 7-10°C, without an extended cold season due to the presence of palms. The presence of palms can give a minimum temperature approximation. In today's climate, palms are only found in places where the MAT is greater than 13°C due to the special plant physiological characteristics that make them sensitive to cold temperatures (Markwick, 1996, 2007). The absolute lowest temperature a palm can tolerate is approximated by a Cold Month Mean Temperature (CMMT) of 5°C, with maybe only a few hours of -10°C (Manchester et al., 2010; Greenwood and Wing, 1995). So, by extension of this modern analog and because Crabtree (1987a, 1987b) found palms, the Two Medicine Formation must have a minimum MAT of 13°C and CMMT of 5°C. Thus, MAT range of 7-10°C, inferred by Crabtree (1987b) using LMA, contradicts that based on the climatic tolerances of modern palms.

Crabtree (1987b) inferred a generalized climate description of megathermal (tropical) and mesothermal, which did not give specific amounts or characteristics of the humidity or precipitation. In the thirty years since the original study, LSI has been

Table 1. MAT and MAP equations calibrated by previous authors. The univariate MAT equations looks at the percent untoothed, while DiLP looks several different parameters. One of these parameters is the Feret Diameter Ratio (FDR), which is the ratio of the Feret diameter and leaf length. Feret Diameter is the diameter of a circle with the same area as the leaf. Tooth Area (TA) to Blade Area (BA) is the combined area of all preserved teeth in ratio to the preserved blade area. Perimeter Ratio (PR) is the ratio between the perimeter of the leaf with teeth and the Internal Perimeter (IP) of the leaf after the teeth are digitally removed. This table and caption was modified from Prue, Upchurch, and Chin, (2015).

Mean Annual Temperature (MAT, in °C)		
Leaf Margin Analysis (LMA) Equations	**SE**	**Authors**
MAT = 4.6 + (% of Untoothed x0.204)	4.8+/-	Peppe et al., 2011 (92 Global sites)
MAT= 5.19 + (% of Untoothed x0.250)	3.01+/-	Royer et al., 2005 (17 test floras; 16 Eastern US and 1 Panama)
MAT= 2.24 + (% of Untoothed x0.286)	2.0 +/-	Wilf, 1997 (9 sites, Western Hemisphere)
MAT= 1.32 + (% of Untoothed x0.29)	0.12+/-	Miller et al., 2006 (84 sites, North & Central America)
MAT= 4.4 + (% of Untoothed x0.306)	0.8+/-	Wolfe, 1979 in Wing and Greenwood, 1993 (31 sites, East Asia)
MAT= 4.694 + (% of Untoothed x0.197)	4.91+/-	Oliver, 2010 (95 Global Sites)
Digital Leaf Physiognomy (DiLP) Equations	**SE**	**Authors**
MAT = -16.004 + (% Untoothed x0.21) + (FDR x42.296) + (# Teeth : IP x - 2.609)	4+/-	Peppe et al., 2011 (92 Global sites)
MAT= 94.95 + (% Untoothed x0.155) + (PR x-84.56) + (TA : BA x- 313.0)	1.99+/-	Royer et al., 2005 (17 test floras; 16 Eastern US and 1 Panama)
MAT = -17.308 + (% Untoothed x 0.255) + (FDR x34.128) + (#Teeth : BA x-0.491)	3.79+/-	Oliver, 2010 (95 Global Sites)

Mean Annual Precipitation (MAP, in cm)		
Leaf Area Analysis (LAA) Equations	**SE(loge, cm)**	**Authors**
MAP = 3.381 + [(ln Leaf Area in mm) x0.22]	0.61 +/-	Oliver, 2010 (95 Global Sites)
MAP = 2.92 + [(ln Leaf Area in mm) x0.283]	0.61 +/-	Peppe et al., 2011 (92 Global sites)
MAP = 0.768 + [(ln Leaf Area in mm) x0.548]	0.359+/-	Wilf et al., 1998 (50 Global sites)
Digital Leaf Physiognomy (DiLP) Equations	**SE(loge, cm)**	**Authors**
MAP = 1.655 + [(ln Leaf Area in mm) x0.449] + [(ln #Teeth : BA) x0.088] + [(ln PR) x-2.34]	0.56 +/-	Oliver, 2010 (95 Global Sites)
MAP = 3.033 + [(ln Leaf Area in mm) x0.298] + [(ln PR) x- 2.717] + [(ln # Teeth : IP) x0.279]	0.27+/-	Peppe et al., 2011 (92 Global sites)

replaced with a more quantitative method called leaf area analysis (LAA) that can give MAP estimates for a given flora. LAA looks at the averaged area of leaves in a flora and correlates it to MAP (Peppe et. al., 2011; Oliver, 2010; Wilf et al., 1998).

Climate Leaf Analysis Multivariate Program (CLAMP)

The previous described methods above are considered univariate methods, while the following two methods are multivariate. Wolfe (1993) proposed a new paleobotanical climate method that looks at multiple physiognomic features that have been correlated to different aspects of the climate. Climate Leaf Analysis Multivariate Program (CLAMP) is a method used by some researchers to estimate paleoclimate (Wolfe, 1993; Teodoridis et al., 2011; Spicer et al., 2011; Yang et al., 2011). CLAMP (Yang et al., 2011) uses canonical correspondence analysis to correlate thirty-six different foliar characteristics of dicot leaves with climatic parameters. Variation in leaf features is correlated to climate characteristics like CMMT and warm month mean temperatures (WMMT), as well as MAT and growing season precipitation (GSP). Different codings have been created in the program to represent the different foliar characteristics, which require training in order to differentiate. The coding of the margins for CLAMP distinguishes at least three different types: toothed, entire, and spinose (considered entire). This method has parameters calibrated to specific hemispheres, with the major calibrations occurring in the larger/major countries' regions, and with one calibration set that combines global data (Yang et al., 2011; Spicer et al., 2004; Yang et al., 2015; Kennedy et al., 2014). As with LMA, a minimum of twenty different morphotypes with near perfect margins is

recommended for this method to be statistically reliable, and the coding parameters must be accurate observational data (Yang et al., 2011).

Digital Leaf Physiognomy (DiLP)

In 2003, Huff et al. described a new multivariate method called Digital Leaf Physiognomy (DiLP), which was later refined to its current form by Royer et al. (2005) and Peppe et al. (2011). This method is a multivariate method like CLAMP that requires a minimum of twenty distinct process-able species/morphotypes with well intact margins that can be reasonably reconstructed. However, it uses fewer foliar characteristics and multiple regression rather than canonical correspondence analysis (Huff et al., 2003; Royer et al., 2005; Peppe et al., 2011). DilP also differs by making direct quantitative measurements of fossil leaves, rather than qualitative characters. DiLP analyzes digital images of specimens to manually calculate the average number of leaf teeth, shape factor, area, and perimeter, and uses different multiple regression equations that correlate these features to temperature and precipitation (Table 1) (Royer, 2012; Peppe et al., 2011), in particular MAT and MAP (Royer et al., 2005). Each DiLP (and LMA) equation is based on different calibrations (see Table 1). The DiLP equations: Royer et al. (2005), Oliver (2010), and Peppe et al. (2011), base their equations on the leaf features that are most correlated to MAT or MAP.

One benefit of the DiLP method, compared to the previously described methods, is the capability of allowing the user to digitally "repair" broken fossil leaves (Royer et al., 2005; Huff et al., 2003). With the added advantage of using computer editing

software to repair missing or broken leaf margins, more climatic details can be obtained than through LMA, LSI and possibly LAA (Royer et al., 2005; Royer, 2012; Prue et al., 2015). Another benefit is the simplicity of coding the foliar characters, since there are only two states for the leaf margin. The margin is either coded as entire or toothed, with spinose being coded as toothed (Royer, 2012; Peppe et al., 2011). Several drawbacks are the complexity of the "repairs" and "cut polygons," and overall time consumption. These draw backs are discussed later.

Sofia Oliver (2010) appears to be the first to test the DiLP method on fossils, which was part of her bachelor's thesis, and later incorporated in Peppe et al. (2011). Her work provided warmer temperature estimates for the Fox Hills, Fort Union, and Hanna Basin formations using DiLP compared to the univariate methods LMA and LAA (Table 2) (Oliver, 2010; Peppe et al., 2011; Prue et al., 2015).

Table 2. Comparison of the climate estimates for the Fox Hills and Two Medicine formations. Fox Hills values are from Peppe et al.'s (2011). The Fox Hills Formation is compared to the Two Medicine Foramtion because these two sites have similar paleolatitude in the same geographic region. MAT estimates for both floras increase significantly when using DiLP. This table was modified from Prue, Upchurch, and Chin (2015).

Paleoclimatological Comaprison						
Formation	Age (Ma)	Paleolatitude	DiLP MAT (°C)	LMA MAT (°C)	DiLP MAP (cm)	LAA MAP (cm)
Fox Hills	66.5	49.7	21.6	14.8	141	152
Two Medicine	79.6	54	18.6	10.5	240.8	162.4

Paleoseasonality

Another purpose of this research is to determine the degree of seasonality of temperature and precipitation as hypothesized by Crabtree (1987b) and Miller et al. (2013). CLAMP can give numerical seasonal estimations, but without more contextual evidence from other proxies, the degree of paleoseasonality is questionable (Yang et al., 2011; Markwick, 2007). In order to determine if there was any degree of paleoseasonality, different proxies need to be identified within the Two Medicine Formation or in formations of similar age and region. Some of these proxies include previously studied paleosols (i.e. fossil soils), dinosaur or other reptile fossils, and fossil plant life forms/taxa.

One prominent utilized geochemical proxy is calcareous paleosols. Calcareous soils are formed when evapotranspiration exceeds precipitation. The calcium occurs in the upper soil horizons where it is mobilized by rainwater and precipitated in lower horizons. As long as evapotranspiration exceeds precipitation, the precipitated calcium will remain in the soil horizons (Mack, 1992). These types of soils are typically associated with arid, semi-arid, and sub-humid environments (Mack, 1992; Buck and Mack, 1995). The major problem with these is that the older they are, the more diagenesis (or chemical alteration) has occurred, which affects chemical analyses (Zhou and Chafetz, 2010; Rogers, 1990). Rogers (1990) described a series caliche layers in association with a mass Hadrosauridae (duckbilled dinosaur) bone bed located in the northern part of the Two Medicine Formation and in the upper section. He hypothesized that these dinosaurs died during an extreme drought event. In contrast to Rogers (1990)

hypothesis, the depositional environment of his fossils and to Crabtree (1987a, 1987b) leaf beds comprises of alluvial and stream deposits. This added description indicates that there was perennial running water with some flooding events. What the evidence from this particular site suggests is that the climate was variable, where it shifted from wet to dry. This could be an indication of seasonality (Rogers 1990) or strong variability on interannual to millennial or longer time scales.

While dinosaur fossils are prominent throughout this formation, there have been some discoveries of fossilized forests near Choteau, Montana (Rogers et al., 1993; Falcon-Lang, 2003; Roberts and Hendrix, 2000). Fossil wood anatomy was analyzed to determine the degree of seasonality within this region. Trees produce annual rings when the vascular cambium stops putting out new growth during times of harsh conditions, whether this be winter, drought or extreme flooding events, and then resumes growth during times of favorable conditions (Falcon-Lang, 2003). Falcon-Lang (2003) examined fossil conifer wood to determine if there was growth interruption. What he found was that there were indeed growth interruptions, but no consistent annual rings to indicate strong temperature seasonality. These types of interruptions are commonly seen in modern tropical climates, where temperatures are relatively consistent. Like in the previous example of caliche, the wood anatomy is not exemplifying a highly variable environment, but one where there was at least a constant temperature of >0°C (Falcon-Lang, 2003).

III. MAIN INQUIRIES OF RESEARCH

The region of interest is the Two Medicine Formation, near Cutbank, Montana. Here I will attempt to define a general regional paleoclimatic reconstruction for this formation. In this research, I attempt to answer these following questions about the formation itself, as well as an in-depth comparison about the methods used in the paleobotanical paleoclimate estimates.

Primary Research Questions

- What was the climate of the lower Two Medicine Formation based on dicot leaf physiognomy?
- What is the range of paleoclimatic estimates for the Two Medicine Formation based on different calibrations of leaf physiognomy?
- What do associated animal fossils (e.g. crocodilians) and sediments (i.e. caliche) say about the seasonality of temperature and precipitation?

Supporting Questions

- Which of the three major leaf methods (e.g. LMA, CLAMP or DiLP) of dicot leaf physiognomy gives the warmest temperature estimate? Which produces the coldest estimate?

- Of the three major leaf physiognomy methods (e.g. LMA, CLAMP or DiLP), which produces temperature estimates most congruent with those from similar-aged floras from the central to northern Western Interior and other regions of North America?

- How much can the coding of leaf margin characters affect the calculated paleoclimate?

- To what extent are estimates of climate based on the leaf physiognomy congruent with those based on climatically restricted plants and animals, sediment type and geochemistry?

IV. METHODS AND MATERIALS

Univariate Methods

I used univariate methods of leaf physiognomy based on linear regression, in particular LMA and LAA. Using digital images of leaves and the descriptive guide of Crabtree's (1987b) thesis, I segregated the entire and non-entire (toothed) margined leaves for LMA. Then using Adobe Photoshop Elements 7.0 (Adobe Systems, San Jose, California, USA) and the scale bar combined with ImageJ (Schindelin et al., 2012; Schneider et al., 2012), I obtained leaf area by digitally separating the leaf from the matrix. Through this process ImageJ (Schindelin et al., 2012; Schneider et al., 2012) directly calculated leaf area, from which I calculated the average for the flora. This average was then put into the LAA equations.

LMA and LAA estimate MAT and MAP, respectively. The regression equations used for MAT and MAP are listed in Table 1. Once separation and measurement were complete, I choose the equation that gives the highest estimation of MAT via LMA and the lowest estimate of MAP via LAA. These univariate methods are documented to give consistently low estimations in MAT and over estimations in MAP respectively (Peppe et al., 2011; Wilf et al., 1997).

Climate Leaf Analysis Multivariate Program (CLAMP)

I used the multivariate method of CLAMP to estimate MAT and other paleoclimate parameters for the Two Medicine Formation. Climate Leaf Analysis Multivariate Program (CLAMP) is a tool created to improve upon temperature and precipitation estimates from LMA and LAA by using multiple qualitative leaf features that have been linked to climate, and is now available online (Yang et al., 2011). These qualitative features are set up as thirty-six presence/absence categories for each morphotype/species. CLAMP requires at least twenty well preserved morphotypes and is an enhancement of LMA (Yang et al., 2011; Wolfe, 1993; and references therein). Crabtree's (1987b) fossil leaf images were evaluated according to the thirty-six listed characteristics in the CLAMP programming. I trained myself to identify all the characteristics used by CLAMP, and then approached this method by breaking it down into three trials, described below. The main idea was to simulate how different researchers may observe the leaf specimens. Several studies have criticized CLAMP because different researchers can identify the same feature as a different characteristic (Huff et al., 2003; Royer et al., 2005; Peppe et al., 2011).

CLAMP's characteristics are separated into groups based on general characteristic types. For example, margin (general characteristic) gives three coding options: 1. Teeth 2. No Teeth 3. Spinose (coded as "No teeth") (Figure 7). If the specimen has teeth, it is further coded to the type of teeth i.e. regular or irregular, close or distant, round or acute, and compounded or minimal compounding (Figure 8). Other coded characteristics are leaf
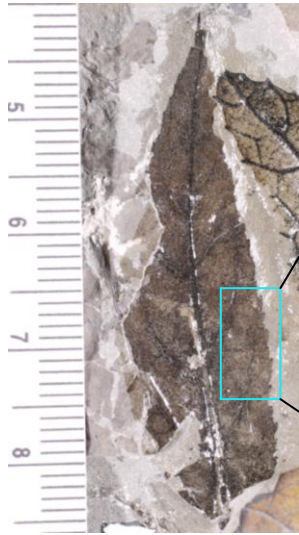
A. Toothed margined as demonstrated by DMNH loc. 1902 16431 Dicot 10
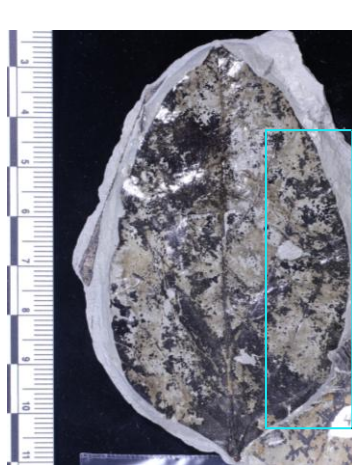
B. Entire margined as demonstrated by DMNH loc. 1902 16426 Dicot 28

C. Spinose (Entire) as demonstrated by the example given by the CLAMP Character definitions. No specimens showed this characteristic. Image taken from the CLAMP Website.

Figure 7. Demonstrates the major margin types that CLAMP codes for. (Wolf, 1993; Yang et al., 2011)

A. Regular teeth
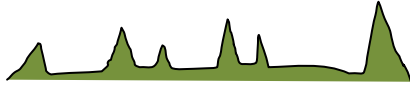
B. Irregular teeth

C. Teeth close to each other

D. Teeth distantly spaced
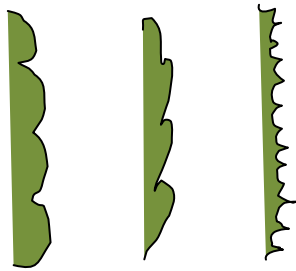
E. Teeth rounded (or appressed)

F. Teeth acute

G. Minor (<50%) compounded teeth

H. Compounded teeth

Figure 8. Line drawings demonstrating the CLAMP teeth characteristics (Yang et al., 2011).

size, apex type, base type, length to width ratio, and shape of leaf (Table 3). For species

that have multiple leaves that exhibit different characters, all features present in the taxon

must be reported (Yang et al., 2011). For example, in Dicots 11 and 25, several leaves

have round teeth, but one or two leaves have acute teeth; these morphotypes were coded

as having both features. This is supposed to represent the full range of characters that a

morphotype possesses because each feature's coding is linked to a numerical portion

associated with the climate parameters. Many of Crabtree's (1987b) morphotypes present

several different features in given categories. Once each of the species was summed up,

the entire flora was automatically averaged for the 36 characteristics (Yang et al., 2011;

Yang et al., 2015; Wolfe, 1993; Kennedy et al., 2014).

Even though it is recommended not to infer or guess leaf characteristics,

numerous Crabtree (1987b) leaf morphotypes did not fit easily into CLAMP's size,

length to width, or leaf shape categories. Where there were severe inconsistencies or

ambiguity, I referred to *The Manual of Leaf Architecture* (Ellis et al., 2009), to create a

modified CLAMP size and shape. To demonstrate the possible differences in my

calibrations, I ran three trials based upon how I categorized the leaves for these

inconsistencies. These trials are described as follows:

1. Initial Processing: how the leaf specimens appeared. It does not follow CLAMP's
   exact rules in size, length to width, and shape.

2. True CLAMP: the coding follows the exact CLAMP Rules for the size, length to
   width, and shape.

3. Inferred Estimate: this coding inferred size, length to width, and shape, while
   following slightly modified CLAMP definition rules.

Table 3. CLAMP Character states as listed in the recommended Excel Worksheet. The first 5 morphotypes are listed and how they are categorized . This is a sample image of the processing excel sheet from the CLAMP website (Yang et al., 2011).

Species / Morphotype	Species Number	Lamina: Unlobed	Lamina: Lobed	Margin: No Teeth	Margin: Teeth	Margin: Teeth Regular	Margin: Teeth Irregular	Margin: Teeth Close	Margin: Teeth Distant	Margin: Teeth Round	Margin: Teeth Acute	Margin: Teeth Compound	Margin: Compound>50%	Size: Nanophyll	Size: Leptophyll I	Size: Leptophyll II	Size: Microphyll I	Size: Microphyll II	Size: Microphyll III	Size: Mesophyll I	Size: Mesophyll II	Size: Mesophyll III	Apex: Emarginate	Apex: Round	Apex: Acute	Apex: Attenuate	Base: Cordate	Base: Round	Base: Acute	L:W <1:1	L:W 1-2:1	L:W 2-3:1	L:W 3-4:1	L:W >4:1	Shape: Obovate	Shape: Elliptic	Shape: Ovate
Dicot 1		1		1	1		1		1	1	1							1	1	1				1	1				1		1	1	1			1	1
Dicot 2	2	1			1		1		1	1																							1				
Dicot 3	3	1		1														1											1				1			1	
Dicot 4	4	1			1	1	1	1		1		1	1					1	1						1			1	1		1	1				1	
Dicot 5	5	1		1																	1			1			1			1						1	

31

In preliminary studies, there was a possibility that some species had weakly spinose teeth. Upon further inspection and detailed definition, we concluded that the teeth were probably true teeth according the CLAMP's definitions.

After the trials were coded, each trial's entire floral characteristics were matched to the closest calibration assemblages to estimate climatic parameters. These calibration assemblages are sets of modern floras from across different regions, continents or the globe used to classify climate parameters due to characteristics that are associated to these regions or continent (i.e. monsoonal conditions in Asia). This study used five of the seven calibrations; the other two are only used when freezing temperatures are suspected, which is not true for our site. The first calibration comes from 144 Non-Freezing Northern Hemisphere Temperature localities correlated with climate recording stations from North America and Asia but does not include alpine floras. An alternative calibration was the same data set combined with gridded metrological data, instead of the climate recording station. Because the Two Medicine Formation locality may have had seasonal precipitation, the Asian Monsoonal calibration was also used because it has an added 45 localities from China. This same data set was later modified to add India and Thailand to make another calibration set. The last calibration used is the Global Calibrations from Six Continents. Samples of modern day plant material came from 378 sites spanning all the continents except Antarctica. Due the individual specifications, each calibration provided its own climate parameter estimates (Yang et al., 2011; Jacques et al., 2011; Khan et al., 2014; Yang et al., 2015; Wolfe, 1993; Kennedy et al., 2014).

Digital Leaf Physiognomy (DiLP)

The other multivariate method used in this study was DiLP. DiLP appeared to be easier to code because there are fewer foliar characters to identify and the margin coding is simpler, i.e. entire or toothed. Instead of just using the fossils as they were, as in CLAMP, four major operations needed to be performed. Directions were followed as outlined in Royer et al. (2005) and Peppe et al. (2011). The first operation was taking photographs of the Crabtree (1987b) leaves at the Denver Museum of Nature and Science (DMNS) during May to July, 2015. DMNS is the current repository for the Crabtree (1987b) leaves from the Two Medicine Formation. Each fossil was photographed with a Canon 5D Mark iii camera attached to a Beseler copy stand that was controlled by Cognisys Stackshot. Photographs were stacked using the program Zerene (Zerene Systems LLC, Richland, Washington, USA) to obtain high-resolution composite images of the fossils with maximum depth of field. Each fossil specimen was focused to emphasize the margins, veins and shape.

The composite images were put into Adobe Photoshop Elements 7.0 (Adobe Systems, San Jose, California, USA) to digitally repair and trace leaf margins, as well as single out the leaves from the matrix. According to Royer et al. (2005), fragmentation loss of 25-50% of the distal leaf end will give a 1.0-1.7°C precision loss in the Root Mean Square. So, only the leaves that had 75% margin preservation or had ~50% margin preservation that followed that mid-vein were selected to be used in this method. These preserved margins were analyzed for presence of teeth. If teeth were found I followed the

selection and removal rules as described in Royer et al., (2005) (Fig 9). The third

operation was to further process these cleaned images in ImageJ (Schindelin et al., 2012;

Schneider et al., 2012), as suggested by Peppe et al. (2011), where automatic

measurements were made using the scale bar and the program's translation ability to

Excel. For the final operation, each of the measurement parameters was averaged for the

species and were then used to calculate the averages for the entire flora. The entire flora

average was then put into the multivariate DiLP regression equations listed in Table 1

(Royer et al., 2005; Oliver, 2010; Peppe et al., 2011).

One of the drawbacks to the DiLP method is the monotonous and time-consuming

task of operation two, the processing of the leaves in Adobe Photoshop Elements 7.0

(Adobe Systems, San Jose, California, USA). Royer et al.'s (2005) directions give

detailed instructions for digitally removing sections of the leaf that have damaged

margins. This cutting and removal of the damaged portions left the user with several

polygons that had to be tediously measured to calculate the desired margin amount. Many

of the polygons were so small that questions arose as to its true usability. Another issue

was that this cutting possibly lost valuable information for the area and perimeter. In

short, a more simplified method that did not waste time and leaf perimeter and area was

warranted.

In order to mitigate these issues, another method was tested to reduce processing

time and leaf perimeter and area loss. I decided to apply the original proposed DiLP

analysis method proposed by Huff et al. (2003), to the fossil leaves. While this method is

not recommended for partially preserved leaves, like fossils (Huff et al., 2003;

A. Entire (Untoothed)

DMNH loc. 1902 16426 Dicot 28
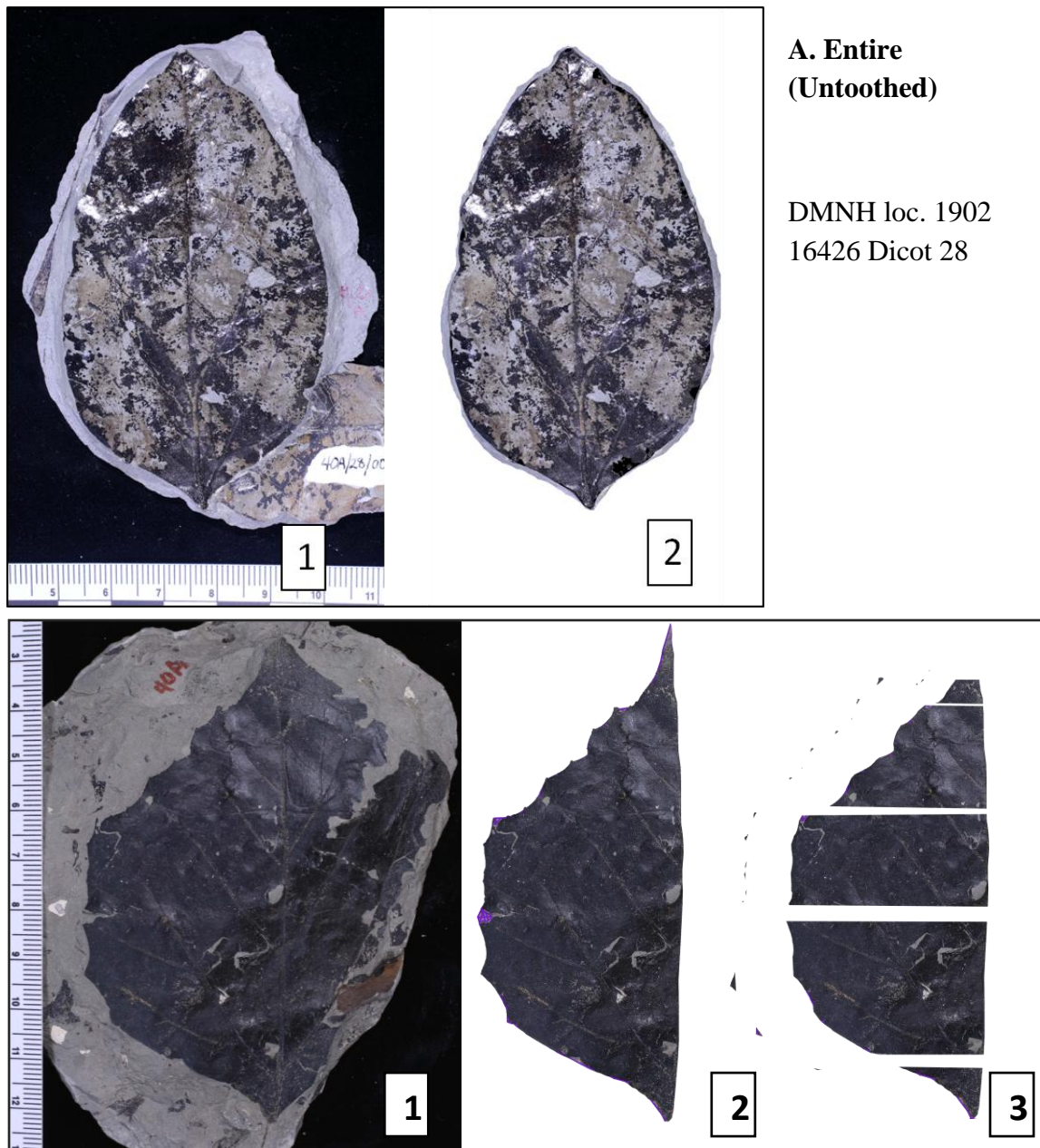
B. Half Toothed   DMNH loc. 1902 16400 Dicot 32

Figure 9. Repaired leaves with using purple lines. **A.**) shows an entire leaf repaired and separated from the matrix. **B.**) shows half of a toothed leaf that is "cut" along the midrib. The image is further processed by removing the teeth. Images in A were presented in Prue, Upchurch, and Chin, (2015).

Royer et al.,2005; Peppe et al.,2011), it is a relatively fast method that minimally reduces perimeter and area. The processing time was shortened because I skipped the step of cutting out the damaged leaf portions, and instead proceeded with the teeth removal step. Another difference from the Royer et al. (2005) approach is that any vascular extension is considered to be a tooth, as long as it is not associated with lobes.

Because Huff et al. (2003) and Royer (personal communication, 2015) advised not to use this method on fossils, I tested to see if the amount of leaf preservation is truly important. Descriptions of the trials were broken down based upon the leaf processing method (i.e. Royer et al. (2005) and Huff et al. (2003)), while the sub trials were based on the amount of area preserved when processed (i.e. Whole, Half and Double Half). "Whole" description is used to describe the process where as much of the leaf is used as possible. For the "Whole Royer" method, this would represent the full method described by Royer et al. (2005), while "Whole Huff" method represents using whole leaves following the methods described by Huff et al. (2003). The description for "Half" refers to leaves where one half of the leaf was heavily damaged and removed. As per the directions of both Royer et al. (2005) and Huff et al. (2003), for leaves where a damaged half was removed, the area of the half was multiplied by two to get total reconstructed blade area. "Half Royer" and "Half Huff" were then processed to the specifications of their individual methods. The final trial "Double Half," took the half leaves described in the previous trial, and using Adobe Photoshop Elements 7.0 (Adobe Systems, San Jose, California, USA), copied and flipped the half leaf's image. These two halves were then lined up and matched along the midvein in an attempt to create a more 'whole' leaf. If the leaves were strongly asymmetrical, then I did not attempt to make a whole leaf, but instead processed the half leaf as per Royer et al. (2005) and Huff et al. (2003) methods.

The "Double Half" leaves were processed as if they were whole leaves. My hypothesis is that the "Double Half" sub-trials should be one of the quicker methods and give similar results to "Whole". Calculations used in this study for the Royer et al. (2005) and Peppe et al. (2011) method can be seen in Table 4, while the calculation for Huff et al. (2003) can be seen in Table 5.

As stated previously, all teeth presented on the leaves were true teeth and were not spinose in nature. Many of the teeth were very small, but due to the presence of glands at the tips, they must be classified as true teeth. Therefore, no further margin classification was needed, beside each method's definition.

Table 4. Physiognomic Variables for fragmentary fossil leaves modifed from Royer et al. (2005) and Peppe et al. (2011)..

*Reconstructed blade area with teeth for leaves where a damaged half was removed, the area of the half was multiplied by two to get total reconstructed blade area.   Equation: (Measured reconstructed blade area of half) x 2

** Inferred perimeter half leaves are calculated by taking the measured perimeter multiplying by two then subtracting the Inferred major axis length multiplied by two.   Equation: (Measured inferred perimeter of half x 2) - (Inferred major axis length of half x 2)

Operation	Variables (abreviation)	Definitions (units)
Basic Terms	Percent untoothed	Percentage of untoothed species in a flora
	*Reconstructed blade area	Area of the reconstructed leaf with the petiole removed (cm^2)
	Number of primary teeth	The number of primary teeth (count)
	Number of secondary teeth	The number of secondary teeth (count)
Layer 1= Reconstucted leaf	Inferred major axis length	Longest measurable line across reconstructed blade area (cm)
	Inferred leaf area with teeth	Reconstructed blade area that has teeth before removal (cm^2)
	Inferred feret's diameter	Diameter of a circle with the same area as reconstructed blade area (cm)
	**Infered Perimeter	Perimeter of the reconstructed leaf (cm)
Layer 2= Damaged Areas Removed	Raw blade area (BA)	Area of the reconstructed leaf after the damaged portions of the margin are removed (cm^2)
	Raw perimeter	Perimeter of reconstructed leaf after the damaged portions of the margin are removed (cm)
	Cut Area	Area of removed damage. Inferred leaf area with teeth minus raw blade area (cm^2)
	Cut Perimeter	Total length of the 'cut' portions of the removed damage area (cm)
Layer 3= Teeth Removed	Number of teeth (# Teeth)	Number of primary and secondary teeth
	Raw internal blade area	Area of the reconstructed leaf after leaf teeth and damaged portions of the margin are removed (cm^2)
	Raw internal perimeter	Perimeter of the reconstructed leaf after leaf teeth and damaged portions of the margin are removed (cm)

Table 4. Continued. Physiognomic Variables for fragmentary fossil leaves modifed from Royer et al. (2005) and Peppe et al. (2011).

	Parameter	Description
Calculated Parameters	Preserved perimeter	Raw perimeter minus the length of the cut perimeter length (cm)
	Preserved internal perimeter (IP)	Raw internal perimeter minus the cut perimeter length (cm)
	Preserved tooth area (TA)	Raw blade area minus raw internal blade area (cm^2)
Calculated Parameter Interactions	Feret's diameter ratio (FDR)	Inferred feret's diameter divided by inferred major axis length (dimensionless)
	Perimeter ratio (PR)	Preserved perimeter divided by preserved internal perimeter (dimensionless)
	Number of teeth / preserved internal perimeter (# Teeth : IP)	Number of teeth divided by the preserved internal perimeter (cm^{-1})
	Preserved tooth area / preserved internal perimeter (TA : IP)	Preserved tooth area divided by preserved internal perimeter (cm)
	Preserved tooth area / raw blade area	Preserved tooth area divided by raw blade area (dimensionless)
	Shape Factor	4π x Inferred leaf area with teeth/Infered Perimeter2 (dimensionless)
	Number of teeth / raw blade area (# Teeth : BA)	Number of teeth divided by raw blade area (cm^{-2})
	Preserved ratio	Raw blade area divided Inferred leaf area with teeth

Table 5. Physiognomic Variables for fragmentary fossil leaves modifed from Huff et al. (2003) and Peppe et al. (2011).

*Reconstructed blade area with teeth for leaves where a damaged half was removed, the area of the half was multiplied by two to get total reconstructed blade area.   Equation: (Measured reconstructed blade area of half) x 2

** Inferred perimeter half leaves are calculated by taking the measured perimeter multiplying by two then subtracting the Inferred major axis l ength multiplied by two.   Equation: (Measured inferred perimeter of half x 2) - (Inferred major axis length of half x 2)

Operation	Variables (abbreviation)	Definitions (units)
Basic Terms	Percent untoothed	Percentage of untoothed species in a flora
	*Reconstructed Blade area	Area of the reconstructed leaf with the petiole removed (cm^2)
	Number of primary teeth	The number of primary teeth (count)
	Number of secondary teeth	The number of secondary teeth (count)
Layer 1= Reconsructed leaf	Inferred major axis length	Longest measurable line across reconstructed blade area (cm)
	Inferred leaf area with teeth (BA)	Reconstructed blade area that has teeth before removal (cm^2)
	Inferred feret's diameter	Diameter of a circle with the same area as reconstructed blade area (cm)
	**Inferred Perimeter	Perimeter of the reconstructed leaf (cm)
Layer 2= Teeth Removed	Inferred leaf area with no teeth	Reconstructed blade area that has teeth after removal (cm^2)
	Leaf perimeter no teeth (IP)	Perimeter of the reconstructed leaf after leaf teeth are removed (cm)
	Number of teeth (# Teeth)	Number of primary and secondary teeth

Table 5. Continued. Physiognomic Variables for fragmentary fossil leaves modifed from Huff et al. (2003) and Peppe et al. (2011).

Calculated Parameters		
	Shape Factor	4π x Inferred leaf area with teeth/Infered Perimeter^2 (dimensionless)
	Feret's diameter ratio (FDR)	Inferred feret's diameter divided by inferred major axis length (dimensionless)
	Tooth area (TA)	Inferred leaf area with teeth minus inferred internal leaf area with no teeth (cm^2)
	Perimeter ratio (PR)	Preserved perimeter divided by Inferred leaf area with no teeth (dimensionless)
	Tooth area / inferred leaf area with no teeth (TA : BA)	Tooth area divided by inferred leaf area with no teeth (dimensionless)
	Number of teeth / Leaf perimeter no teeth (# Teeth : IP)	Number of teeth divided by the leaf perimeter no teeth (cm^{-1})
	Number of teeth /Inferred leaf area with teeth (# Teeth : BA)	Number of teeth divided by inferred leaf area with teeth (cm^{-2})
	Preserved ratio	Inferred leaf area without teeth divided inferred leaf area with teeth

V. RESULTS

Leaf Margin Analysis (LMA)

The angiosperm specimens from the Two Medicine Formation collected by David Crabtree (1987a,1987b) yielded 88 total specimens belonging to 41 morphotypes, based upon Crabtree's (1987b) and my categorization and the leaf selection criteria outlined on the CLAMP website and by Royer et al. (2005). However, only a maximum of 38 woody dicot morphotypes was processed in any of the methods. From these morphotypes, I concluded that an estimated 29% of the species were entire margined, with two species identified as 50% toothed Table 6 and Table 7. Using this percentage in the LMA equations listed in Table 1, LMA gives an equation-dependent range of 8-12°C for the paleoclimate. The lowest LMA temperature estimate of 8°C was based on Wilf's equation (1997b), while the high estimate of 12°C comes from Royer et al.'s calculations (2005). Wolf's original equation (1979; Wing and Greenwood, 1993), which became the basis for the CLAMP program, provides a temperature estimate of 10°C. Crabtree's (1987b) estimate using Wolf (1978) was also 10°C.

Table 6. Crabtree's specimens and the methods that they were used in.
T=Teeth; E= Entire for LMA. The three columns LAA, CLAMP and DiLP are marked
with a "Y" for yes those specimens were used in those methods. "N" for not used.

Specimen #	Label	LMA	LAA	CLAMP	DiLP
1	DMNH Dicot 01 loc 1902 27A-01-003	T	N	Y	N
2	DMNH Dicot 01 loc 1902 25A-01	T	N	Y	N
3	DMNH Dicot 01 loc 1902 27A-01-004	T	Y	Y	Y
4	DMNH Dicot 01 loc 1902 27A-01-006	T	N	Y	N
5	DMNH Dicot 01 loc 1902 16414	E	Y	Y	Y
6	DMNH Dicot 01 loc 1902 16415	E	N	Y	N
7	DMNH Dicot 01 loc 1902 16416	E	N	Y	N
8	DMNH Dicot 01 loc 1902 16417	T	N	Y	N
9	DMNH Dicot 01 loc 1902 16418	T	Y	Y	Y
10	DMNH Dicot 02 loc 1902 16432	T	N	Y	N
11	DMNH Dicot 03 loc 1902 41A-03-003	E	N	Y	N
12	DMNH Dicot 03 loc 1902 39A-03-002	E	Y	Y	Y
13	DMNH Dicot 03 loc 1902 40A-03-005	E	N	Y	N
14	DMNH Dicot 03 loc 1902 16429	E	N	Y	N
15	DMNH Dicot 04 loc 1902 16368 -002	T	Y	Y	Y
16	DMNH Dicot 04 loc 1902 16368 -003	T	N	Y	N
17	DMNH Dicot 04 loc 1902 16368 -004	T	N	Y	N
18	DMNH Dicot 04 loc 1902 16369	T	Y	Y	Y
19	DMNH Dicot 05 loc 1902 16425	E	Y	Y	Y
20	DMNH Dicot 06 loc 1902 16405	T	Y	Y	Y
21	DMNH Dicot 06 loc 1902 16406	T	N	Y	N
22	DMNH Dicot 06 loc 1902 16420	T	Y	Y	Y
23	DMNH Dicot 07 loc 1902 42A-07-001	E	Y	Y	Y
24	DMNH Dicot 09 loc 1902 40A-09-001	T	Y	Y	Y
25	DMNH Dicot 10 loc 1902 16431	T	Y	Y	Y
26	DMNH Dicot 11 loc 1902 16202	T	N	Y	N
27	DMNH Dicot 11 loc 1902 16210	T	N	Y	N
28	DMNH Dicot 11 loc 1902 16211	T	N	Y	N
29	DMNH Dicot 11 loc 1902 16220	T	N	Y	N
30	DMNH Dicot 11 loc 1902 16338	T	N	Y	N
31	DMNH Dicot 11 loc 1902 16394	T	N	Y	N
32	DMNH Dicot 11 loc 1902 16396	T	Y	Y	Y
33	DMNH Dicot 12 loc 1902 16366	T	N	Y	N
34	DMNH Dicot 14 loc 1902 16370	BAD	BAD	BAD	BAD
35	DMNH Dicot 15 loc 1902 16365	T	N	Y	N
36	DMNH Dicot 16 loc 1902 16367	E	N	Y	N
37	DMNH Dicot 17 loc 1902 16427	T	Y	Y	Y
38	DMNH Dicot 19 loc 1902 16410	E	N	Y	N
39	DMNH Dicot 25 loc 1902 16389	T	N	Y	N
40	DMNH Dicot 25 loc 1902 16273	T	N	Y	N
41	DMNH Dicot 25 loc 1902 16275	T	Y	Y	Y
42	DMNH Dicot 25 loc 1902 16281	T	Y	Y	Y
43	DMNH Dicot 25 loc 1902 16292	T	Y	Y	Y
44	DMNH Dicot 25 loc 1902 16388	T	Y	Y	Y

Table 6. Continued. Crabtree's Specimens and the methods that they were used in.

45	DMNH Dicot 25 loc 1902 16409 A	T	Y	Y	Y
46	DMNH Dicot 25 loc 1902 16409 B	T	N	Y	N
47	DMNH Dicot 25 loc 1902 16409 C	T	N	Y	N
48	DMNH Dicot 27 loc 1902 16371	T	Y	Y	Y
49	DMNH Dicot 27 loc 1902 16372	T	N	Y	N
50	DMNH Dicot 27 loc 1902 16374	T	N	Y	N
51	DMNH Dicot 28 loc 1902 16389	E	Y	Y	Y
52	DMNH Dicot 28 loc 1902 16426	E	Y	Y	Y
53	DMNH Dicot 29 loc 1902 16412	BAD	BAD	BAD	BAD
54	DMNH Dicot 30 loc 1902 16419	T	Y	Y	Y
55	DMNH Dicot 31 loc 1902 40A-31	T	N	Y	N
56	DMNH Dicot 31 loc 1902 16419	T	N	Y	N
57	DMNH Dicot 32 loc 1902 16428	T	N	Y	N
58	DMNH Dicot 32 loc 1902 16398	BAD	BAD	BAD	BAD
59	DMNH Dicot 32 loc 1902 16400	T	Y	Y	Y
60	DMNH Dicot 32 loc 1902 16402	T	Y	Y	Y
61	DMNH Dicot 32 loc 1902 16403	T	N	Y	N
62	DMNH Dicot 32 loc 1902 16404	T	N	Y	N
63	DMNH Dicot 32 loc 1902 16399	T	N	Y	N
64	DMNH Dicot 33 loc 1902 16430	T	N	Y	N
65	DMNH Dicot 36 loc 1902 26A-36-002	T	N	Y	N
66	DMNH Dicot 36 loc 1902 16407	T	N	Y	N
67	DMNH Dicot 40 loc 1902 16413	E	N	Y	N
68	DMNH Dicot 43 loc 1902 16411	E	Y	Y	Y
69	DMNH Dicot 44 loc 1902 40A-44-011	E	N	Y	N
70	DMNH Dicot 44 loc 1902 39A-44-005	T	Y	Y	Y
71	DMNH Dicot 44 loc 1902 40A-44-	T	N	Y	N
72	DMNH Dicot 50 loc 1902 16390	T	N	Y	N
73	DMNH Dicot 50 loc 1902 16392	T	N	Y	N
74	DMNH Dicot 53 loc 1902 16397	T	Y	Y	Y
75	DMNH Dicot 57 loc 1902 38A-57-	E	N	Y	N
76	DMNH Dicot 57 loc 1902 16422	E	N	Y	N
77	DMNH Dicot 57 loc 1902 16423	E	Y	Y	Y
78	DMNH Dicot 57 loc 1902 16424	E	Y	Y	Y
79	DMNH Dicot Unknown 1 loc 1902 16	T	Y	Y	Y
80	DMNH Dicot Unknown 2 loc 1902 16	T	N	Y	N
81	DMNH Dicot Unknown 3 loc 1902 16	T	Y	Y	Y
82	DMNH Dicot Unknown 4 loc 1902 42	BAD	BAD	BAD	BAD
83	DMNH Dicot Unknown 5 loc 1902 16	T	Y	Y	Y
84	DMNH Dicot Unknown 6 loc 1902 16	T	N	Y	N
85	DMNH Dicot Unknown 7 loc 1902 16	T	N	Y	N
86	DMNH Dicot Unknown 8 loc 1902 16	T	Y	Y	Y
87	DMNH Dicot Unknown 9 loc 1902 40	T	N	Y	N
88	DMNH Dicot Unknown 10 loc 1902 1	T	N	Y	N

Table 7. Margin type of the identified morphotypes. 1 is the dummy variable for entire, 0.5 represents half the specimens of that morphotype had teeth, while 0 is for morphotypes that have teeth.

Total Dicots	
Name	Margin type
Dicot 1	0.5
Dicot 2	0
Dicot 3	1
Dicot 4	0
Dicot 5	1
Dicot 6	0
Dicot 7	1
Dicot 9	0
Dicot 10	0
Dicot 11	0
Dicot 12	0
Dicot 15	0
Dicot 16	1
Dicot 17	0
Dicot 19	1
Dicot 25	0
Dicot 27	0
Dicot 28	1
Dicot 30	0
Dicot 31	0
Dicot 32	0
Dicot 33	0
Dicot 36	0
Dicot 40	1
Dicot 43	1
Dicot 44	0.5
Dicot 50	0
Dicot 53	0
Dicot 57	1
Unknown 1	0
Unknown 2	0
Unknown 3	0
Unknown 5	0
Unknown 6	0
Unknown 7	0
Unknown 8	0
Unknown 9	1
Unknown 10	0
Percent entire:	**28.9**

Climate leaf Analysis Multivariate Program (CLAMP)

Climate Leaf Analysis Multivariate Program (CLAMP) is a tool created to improve upon temperature estimates from LMA, by using qualitative leaf features that have been linked to climate, and it is now possible to use this approach through an online database (Yang et al., 2011). These qualitative features are set up as 36 presence/absence categories designated for each morphotype/species. Because of the ambiguity of classification of size and shape, along with user perception, three main trials were run to try to see what the variation in climate estimates were. The trials, described above, are: Initial Processing, True CLAMP, and Inferred Estimate. Each of these trials was then processed in the climate calibrations. The CLAMP website offers seven different climate calibrations that are based on modern day floral sites. This study used five of the seven calibrations because the other two are used when freezing temperatures are suspected, which is not true for our site (Yang et al., 2011). The following results are listed in Table 8. Minimum and maximum range estimates of the climate parameters for each sub-trial, across all calibration sites, are listed in Table 9.

-Initial Processing

The first trial was run as it was initially presented. Depending which of the four calibration sites was used, MAT ranged from 11-15°C, and the GSP ranged from 76-107 cm. WMMT ranged from 20-23°C, while CMMT ranged from 2-7°C. Precipitation for the Three Wet Months was 53-68cm, while precipitation for the Three Dry Months was

Table 8. Climate parameter estimates of the sub-trials in the five different CLAMP calibration data sets.

Non-Freezing Northern Hemisphere Temperature Localities Calibration (Physg3brcAZ.MET)

CLAMP Sub-trial	Completeness	MAT (°C)	Uncertainties	WMMT (°C)	Uncertainties	CMMT (°C)	Uncertainties	GSP (cm)	Uncertainties	Three WET Months Precip (cm)	Uncertainties	Three DRY Months Precip (cm)	Uncertainties
Initial Processing	0.68	13.2	2	20.77	2.7	6.41	3.4	107.4	48.3	52.55	20.6	19.1	13.7
Initial Processing Dicot 6 add fix	0.68	13.23	2	20.77	2.7	6.46	3.4	108.45	48.3	53.02	20.6	19.34	13.7
Initial Processing Dicot 6 delete fix	0.68	13.27	2	20.77	2.7	6.53	3.4	108.17	48.3	52.96	20.6	19.37	13.7
True CLAMP Rules	0.26	13.08	2	20.96	2.7	5.98	3.4	123.44	48.3	59.46	20.6	23.12	13.7
True CLAMP Rules Dicot 6, 25 add fix	0.26	13.36	2	20.86	2.7	6.6	3.4	126.31	48.3	60.82	20.6	23.81	13.7
True CLAMP Rules Dicot 6, 25 delete fix	0.26	13.54	2	20.8	2.7	7	3.4	125.77	48.3	60.65	20.6	23.63	13.7
Inferred Estimate	0.56	13.43	2	21.29	2.7	6.4	3.4	135	48.3	63.11	20.6	23.3	13.7
Inferred Estimate Dicot 6,11,36 add fix	0.56	13.6	2	21.22	2.7	6.77	3.4	138.31	48.3	64.56	20.6	24.04	13.7
Inferred Estimate Dicot 6,11,36 delete fix	0.56	13.91	2	21.26	2.7	7.35	3.4	135.91	48.3	63.91	20.6	23.95	13.7

CLAMP Processing code: 6F086E4ECA163AC8

Non-Freezing Northern Hemisphere Temperature Localities with Gridded Metrological Data Calibration (Physg3brcAZ GRIDMET)

CLAMP Sub-trial	Completeness	MAT (°C)	Uncertainties	WMMT (°C)	Uncertainties	CMMT (°C)	Uncertainties	GSP (cm)	Uncertainties	Three WET Months Precip (cm)	Uncertainties	Three DRY Months Precip (cm)	Uncertainties
Initial Processing	0.68	13.14	2.1	20.47	2.5	6.12	3.4	99.7	31.7	64.09	22.9	16.33	5.9
Initial Processing Dicot 6 add fix	0.68	13.17	2.1	20.46	2.5	6.17	3.4	100.72	31.7	64.38	22.9	16.51	5.9
Initial Processing Dicot 6 delete fix	0.68	13.23	2.1	20.5	2.5	6.24	3.4	101.03	31.7	64.19	22.9	16.69	5.9
True CLAMP Rules	0.26	12.64	2.1	20.33	2.5	5.25	3.4	107.69	31.7	69.36	22.9	16.44	5.9
True CLAMP Rules Dicot 6, 25 add fix	0.26	12.95	2.1	20.3	2.5	5.82	3.4	113.45	31.7	70.4	22.9	17.72	5.9
True CLAMP Rules Dicot 6, 25 delete fix	0.26	13.12	2.1	20.37	2.5	6.09	3.4	114.94	31.7	70.23	22.9	18.18	5.9
Inferred Estimate	0.56	13.01	2.1	20.63	2.5	5.76	3.4	111.17	31.7	70.84	22.9	16.07	5.9
Inferred Estimate Dicot 6,11,36 add fix	0.56	13.19	2.1	20.59	2.5	6.1	3.4	115.63	31.7	71.88	22.9	16.97	5.9
Inferred Estimate Dicot 6,11,36 delete fix	0.56	13.57	2.1	20.76	2.5	6.66	3.4	117.84	31.7	70.96	22.9	17.92	5.9

CLAMP Processing code: 8A28C23EAD2D598

Asian Monsoonal Regions Calibration (PhysgAsia1)

CLAMP Sub-trial	Completeness	MAT (°C)	Uncertainties	WMMT (°C)	Uncertainties	CMMT (°C)	Uncertainties	GSP (cm)	Uncertainties	Three WET Months Precip (cm)	Uncertainties	Three DRY Months Precip (cm)	Uncertainties
Initial Processing	0.68	12.74	2.5	21.69	3.0	5.15	4.1	100.15	49.7	68.02	23.9	19.13	10.4
Initial Processing Dicot 6 add fix	0.68	12.76	2.5	21.68	3.0	5.2	4.1	100.7	49.7	68.33	23.9	19.21	10.4
Initial Processing Dicot 6 delete fix	0.68	12.8	2.5	21.7	3.0	5.23	4.1	100.37	49.7	68.07	23.9	19.04	10.4
True CLAMP Rules	0.26	12.43	2.5	21.85	3.0	4.38	4.1	103.65	49.7	69.34	23.9	19.36	10.4
True CLAMP Rules Dicot 6, 25 add fix	0.26	12.65	2.5	21.87	3.0	4.7	4.1	105.4	49.7	70.05	23.9	19.25	10.4
True CLAMP Rules Dicot 6, 25 delete fix	0.26	12.75	2.5	22.07	3.0	4.65	4.1	104.54	49.7	68.95	23.9	18.61	10.4
Inferred Estimate	0.56	12.94	2.5	22.09	3.0	5.19	4.1	107.13	49.7	70.25	23.9	19.69	10.4
Inferred Estimate Dicot 6,11,36 add fix	0.56	13.06	2.5	22.07	3.0	5.4	4.1	109	49.7	71.21	23.9	19.82	10.4
Inferred Estimate Dicot 6,11,36 delete fix	0.56	13.33	2.5	22.26	3.0	5.62	4.1	107	49.7	69.48	23.9	18.73	10.4

CLAMP Processing code: 6CD2C57616DEF0

Table 8. Campanian. Climate parameter estimates of the sub-trials in the five different CLAMP calibration data sets.

| | | | | | | | | | | Three WET Months | | Three DRY Months | |
CLAMP Sub-trial	Completeness	MAT (°C)	Uncertainties	WMMT (°C)	Uncertainties	CMMT (°C)	Uncertainties	GSP (cm)	Uncertainties	Precip (cm)	Uncertainties	Precip (cm)	Uncertainties
Initial Processing	0.68	14.9	2.3	22.78	2.8	7.4	3.6	106.27	60.6	64.38	35.8	14.23	9.5
Initial Processing Dicot 6 add fix	0.68	14.92	2.3	22.77	2.8	7.43	3.6	107.2	60.6	64.64	35.8	14.4	9.5
Initial Processing Dicot 6 delete fix	0.68	14.96	2.3	22.72	2.8	7.55	3.6	106.28	60.6	64.67	35.8	14.13	9.5
True CLAMP Rules	0.26	14.89	2.3	23.45	2.8	6.71	3.6	114.9	60.6	67.54	35.8	14.34	9.5
True CLAMP Rules Dicot 6, 25 add fix	0.26	15.13	2.3	23.3	2.8	7.22	3.6	115.41	60.6	68.7	35.8	13.96	9.5
True CLAMP Rules Dicot 6, 25 delete fix	0.26	15.34	2.3	23.42	2.8	7.5	3.6	112.13	60.6	69.11	35.8	12.5	9.5
Inferred Estimate	0.56	15.34	2.3	23.59	2.8	7.44	3.6	120.33	60.6	67.05	35.8	16.12	9.5
Inferred Estimate Dicot 6,11,36 add fix	0.56	15.46	2.3	23.49	2.8	7.71	3.6	122.16	60.6	68.02	35.8	16.27	9.5
Inferred Estimate Dicot 6,11,36 delete fix	0.56	15.78	2.3	23.28	2.8	8.47	3.6	116.58	60.6	68.26	35.8	14.38	9.5

Asian Monsoonal Regions Including India and Thailand Calibrations (PhysgAsia2)

CLAMP Processing code: 764AD23E9DB0F8E4

| | | | | | | | | | | Three WET Months | | Three DRY Months | |
CLAMP Sub-trial	Completeness	MAT (°C)	Uncertainties	WMMT (°C)	Uncertainties	CMMT (°C)	Uncertainties	GSP (cm)	Uncertainties	Precip (cm)	Uncertainties	Precip (cm)	Uncertainties
Initial Processing	0.68	11.46	4.0	21.92	3.9	1.63	6.7	76.02	54.9	53.11	32.2	8.8	13.0
Initial Processing Dicot 6 add fix	0.68	11.53	4.0	21.93	3.9	1.76	6.7	76.94	54.9	53.33	32.2	8.89	13.0
Initial Processing Dicot 6 delete fix	0.68	11.57	4.0	21.98	3.9	1.8	6.7	77.07	54.9	53.54	32.2	8.81	13.0
True CLAMP Rules	0.26	11.6	4.0	22.04	3.9	1.69	6.7	80.22	54.9	55.02	32.2	8.76	13.0
True CLAMP Rules Dicot 6, 25 add fix	0.26	12.1	4.0	22.3	3.9	2.39	6.7	83.64	54.9	56.68	32.2	8.68	13.0
True CLAMP Rules Dicot 6, 25 delete fix	0.26	12.35	4.0	22.68	3.9	2.37	6.7	81.46	54.9	57.8	32.2	7.86	13.0
Inferred Estimate	0.56	11.72	4.0	22.33	3.9	1.52	6.7	78.06	54.9	54.15	32.2	8.18	13.0
Inferred Estimate Dicot 6,11,36 add fix	0.56	12.07	4.0	22.46	3.9	2.08	6.7	81.23	54.9	55.27	32.2	8.28	13.0
Inferred Estimate Dicot 6,11,36 delete fix	0.56	12.28	4.0	22.77	3.9	2.06	6.7	81.04	54.9	56.46	32.2	7.76	13.0

Global Calibrations From Six Continents (the PhysgGlobal)

CLAMP Processing code: 16C3DECB7DCB7124

Table 9. The Minimum and maximum estimates for each climate parameter from across all the CLAMP calibration sites.

Sub-Trial	Completeness	MAT °C		GSP (cm)		WMMT °C		CMMT °C		Three WET Month Precip (cm)		Three DRY Month Precip (cm)	
		Low	High	Low	High	Low	High	Low	High	Low	High	Low	High
Initial Processing	0.68	11.46	14.9	76.02	107.4	20.47	22.78	1.63	7.4	52.55	68.02	8.8	19.13
Initial Processing Dicot 6 add fix	0.68	11.53	14.92	76.94	108.45	20.46	22.77	1.76	7.43	53.02	68.33	8.89	19.34
Initial Processing Dicot 6 delete fix	0.68	11.57	14.96	77.07	108.17	20.5	22.72	1.8	7.55	52.96	68.07	8.81	19.37
True CLAMP Rules	0.26	11.6	14.89	80.22	123.44	20.33	23.45	1.69	6.71	55.02	69.36	8.76	23.12
True CLAMP Rules Dicot 6, 25 add fix	0.26	12.1	15.13	83.64	126.31	20.3	23.3	2.39	7.22	56.68	70.4	8.68	23.81
True CLAMP Rules Dicot 6, 25 delete fix	0.26	12.35	15.34	81.46	125.77	20.37	23.42	2.37	7.5	57.8	70.23	7.86	23.63
Inferred Estimate	0.56	11.72	15.34	78.06	135	20.63	23.59	1.52	7.44	54.15	70.84	8.18	23.3
Inferred Estimate Dicot 6,11,36 add fix	0.56	12.07	15.46	81.23	138.31	20.59	23.49	2.08	7.71	55.27	71.88	8.28	24.04
Inferred Estimate Dicot 6,11,36 delete fix	0.56	12.28	15.78	81.04	135.91	20.76	23.28	2.06	8.47	56.46	70.96	7.76	23.95

9-19cm. The total leaves for this full trial filled 68 % of the required categories. When running this trial, there was an error message in the sizing for the three leaves of Dicot 6. To combat this error, sub-trials were run.

The first sub-trial scored the empty size character (Micro 3) that falls between the two problem Dicot 6 leaves. Doing this changed the MAT range was 12-15°C, while the GSP range was 77-108 cm. WMMT was 20-23°C and CMMT was 2-7°C. Three Wet Months amount range was 53-68cm and the Three Dry Months amount range was 9-19cm.

The second sub-trial was where the smallest (Micro 2) of the leaves, DMNH loc. 1902 16405 Dicot 6, and its associated features were removed. The estimated MAT range was 13-15°C and the GSP range was 77-108 cm. WMMT was 21-23°C and the CMMT was 2-8°C. Three Wet Months amount was 53-68cm, while the Three Dry Months amount was 9-19cm.

-True CLAMP

True CLAMP was set up to run follow the rules of CLAMP classification to the strictest. This is to help test ambiguity that maybe associated with different users. Again, based on all the calibrations used, the MAT estimate ranged from 12-15°C. The GSP was 80-123 cm. Seasonality signals for temperature ranged 20-23°C for WMMT and 2-7°C for CMMT. Precipitation seasonality signal ranged 55-69cm for the Three Wet Months Precipitation, while 9-23cm for the Three Dry Months Precipitation. The total leaves for this trial filled 26% of the required categories.

Like in the previous set, CLAMP identified errors in the size categories. Size category errors were on Dicot 6 and Dicot 25. We added the sizes Micro 3 to Dicot 6 and Meso 2 to Dicot 25. The estimates from this sub-trial are as follows: MAT range was 12-15°C and GSP range was 84-126 cm. Seasonality temperature estimates for WMMT was 20-23°C and CMMT was 2-7°C. Precipitation seasonality for the Three Wet Months precipitation was 57-70 cm and Three Dry Months precipitation was 9-24 cm.

In the next sub-trial, I removed the small leaf, Micro 2) from Dicot 6 (DMNH loc. 1902 16405) and the two small leaves, Micro 3 and Meso 1, from Dicot 25 (DMNH loc.1902 16275 and DMNH loc.1902 16388). The responding MAT range was 12-15°C and the GSP was 81-126 cm. WMMT was 20-23°C and the CMMT was 2-8°C. Three Wet Months precipitation was 58-70 cm and Three Dry Months precipitation was 8-24 cm.

-Inferred Estimate

The final set of sub-trials was based off my extrapolated sizes of the leaves when context clues of the angles of the margins were used. Based on which calibration used, the MAT range for this set of data was 12-15°C, while the GSP range was 78-135 cm. WMMT ranged from 21-34°C, while CMMT ranged from 2-7°C. Three Wet Months precipitation was 54-71 cm, while Three Dry Months precipitation was 8-23cm. Total leaves for this trial filled 56% of the required categories.

Errors in the size categories were present in Dicot 6, Dicot 11, and Dicot 36. Size category Micro3 was added to each of these dicots and Meso1 was also added to Dicot

11. The climate estimate range for MAT was 12-15°C while GSP range was 81-138 cm. WMMT was 21-23°C for and CMMT was 2-8°C. Three Wet Months precipitation was 55-72cm and Three Dry Months precipitation was 8-24cm.

The smaller leaves with errors, DMNH loc. 1902 specimen numbers 16405 Dicot 6, 16220 Dicot 11, and 26A/36/002, and their associated features were removed. For the final sub-trial a MAT of 12-16°C and the GSP range was 81-136 cm were estimated. Seasonality parameters for WMMT was 21-23°C and the CMMT was 2-9°C. The Three Wet Months precipitation estimate was 56-71cm, while the Three Dry Months precipitation estimate was 8-34cm.

Digital Leaf Physiognomy (DiLP)

As noted above, one of the major problems with CLAMP is the inconsistency in defining characters. This was the major reason for creating Digital Leaf Physiognomy (DiLP) (Huff et al., 2003; Royer et al. 2005). DiLP was created to offset user ambiguity of leaf characteristics by quantifying important climate-related leaf characteristics. One of the draw backs to this method is the requirement for the leaves to be in almost pristine condition. I was able to analyze 34 specimens from 23 proposed morphotypes using Royer et al.'s (2005) method. The percent entire margined used in the DiLP calculations required the utilization all 38 morphotypes, not just the 23 morphotypes used for processing.

Six different ways (sub-trials), of utilizing fossil leaf data were used, as outlined above in the methods. Three follow Royer et al.'s (2005) analysis, while the other three

follow the older proposed method by Huff et al. (2003). Each version of the two methods

estimated climate parameters from different preservation percentages of certain damaged

leaves. Whole, Half and Double Half refer to different approaches which utilize different

amounts of fossil leaf areas; Whole, is part of the original proposed method. Half is

where one half of the leaf is good, and if the other half has less than 50% preserved, that

half is removed. The Double Half is taking the good half from the Half and carbon

copying it and matching the two sides along the mid-vein. Once these determinations

have been completed, the data are then averaged for the morphotype and site, as per

Royer et al. (2005) (Table 10). These versions were then put into the DiLP equations

listed in Table 1. The following results are listed in Tables 11 and 12.

Table 10. Site averages for each parameter for all 38 dicots for each DiLP processing
method

Site averages of each parameter for all 38 dicots of the Two Medicine Formation							
Processing Method	Portion of Untoothed	Feret Diameter Ratio	#Teeth: IP	Perimeter Ratio	Tooth Area (TA): Blade Area (BA)	# of Teeth : Blade Area	Leaf Area [mm^2]
Whole Royer	28.9 % Untoothed	1.04	6.00	1.13	0.025	7.51	2137.2
Half Royer	28.9 % Untoothed	1.04	5.95	1.13	0.025	7.22	2150.5
Double Half Royer	28.9 % Untoothed	1.05	5.86	1.13	0.025	7.39	2157.7
Whole Huff	28.9 % Untoothed	1.04	3.19	1.06	0.010	4.94	2137.2
Half Huff	28.9 % Untoothed	1.04	3.25	1.07	0.011	5.14	2150.5
Double Half Huff	28.9 % Untoothed	1.05	3.23	1.06	0.010	5.01	2157.7

Table 11. Mean annual temperature (MAT) estimates for the Two Medicine Formation from equation models.

Leaf Margin Analysis (LMA) Equations	MAT (°C)	SE
Royer et al 2005	12.43	3.01+/-
Peppe et al 2011	10.51	4.8+/-
Wolfe 1979, Wing and Greenwood, 1993	10.00	0.8+/-
Miller et al. 2006 LMA	9.71	0.12+/-
Wilf 1997 LMA	8.16	3.4+/-
Oliver 2010	10.40	4.91+/-

Digital Leaf Physignomy (DiLP) Equations	Whole Royer	Half Royer	Double Half Royer	Whole Huff	Half Huff	Double Half Huff	SE
Peppe et al 2011 Equation	19	19	19	26	26	26	4+/-
Royer et al 2005 Equation	12	11	12	13	13	13	1.99+/-
Oliver 2010 Equation	22	22	22	23	23	24	3.79+/-

54

Table 12. Mean annual precipitation (MAP) estimates for the Two Medicine Formation from equation models. SE are uneven due to be converted from loge.

Equation Models	Whole Royer MAP (cm)	Lower SE	Upper SE	Half Royer MAP (cm)	Lower SE	Upper SE	Double Half Royer MAP (cm)	Lower SE	Upper SE
Leaf Area Analysis (LAA) Equations									
Peppe et al 2011	162.36	-74.14	136.46	162.65	-74.27	136.69	162.80	-74.34	136.82
Oliver 2010	158.82	-72.53	133.48	159.04	-72.63	133.66	159.16	-72.68	133.76
Wilf et al 1998	143.98	-43.43	62.18	144.47	-43.58	62.40	144.73	-43.66	62.51
Digital Leaf Physignomy (DiLP) Equations									
Peppe et al 2011 Equation:	240.81	-56.98	74.64	240.10	-56.81	74.42	240.46	-56.90	74.53
Oliver 2010	146.59	-62.68	109.74	146.18	-62.68	109.74	147.31	-63.17	110.59

Equation Models	Whole Huff MAP (cm)	Lower SE	Upper SE	Half Huff MAP (cm)	Lower SE	Upper SE	Double Half Huff MAP (cm)	Lower SE	Upper SE
Leaf Area Analysis (LAA) Equations									
Peppe et al 2011	162.36	-74.14	136.46	162.65	-74.27	136.69	162.80	-74.34	136.82
Oliver 2010	158.82	-72.53	133.48	159.04	-72.63	133.66	159.16	-72.68	133.76
Wilf et al 1998	143.98	-43.43	62.18	144.47	-43.58	62.40	144.73	-43.66	62.51
Digital Leaf Physignomy (DiLP) Equations									
Peppe et al 2011 Equation:	239.82	-56.75	74.34	238.48	-56.43	73.92	239.68	-56.71	74.29
Oliver 2010	163.88	-70.27	123.02	163.06	-69.92	122.41	163.75	-70.21	122.92

- Royer et al. (2005)

The "Whole Royer" approach, following the original Royer et al. (2005) method, was used on six specimens from six different morphotypes that only preserved a half leaf. This is roughly 17% of the processed specimens and 26% of the morphotypes containing a half leaf. Using the site averages obtained from this version (Table 10), and putting them into the DiLP MAT equations to get a range of 12-22°C. Oliver (2010) DiLP MAT equation gave the highest estimate of 22°C, while Royer et al. (2005) gave the lowest estimate of 12°C. When the site averages were put into DiLP MAP equations the range was 147-241 cm/year. Oliver (2010) DiLP MAP equation gave the lowest estimate, while Peppe et al. (2011) MAP equation gave the highest. The loss ratio, the loss between the inferred blade area and raw blade area after the damage has been removed, is 34%.

In order to search and test for a simpler processing method than that of Royer et al. (2005), I decided to process the better preserved half of the leaf--that is, to use the "Half Royer" approach. Out of the 34 specimens used, 35% of them were half leaves, which were present in about 43% of the species. Using the site averages from this processing, the DiLP MAT estimate ranged from 11-22°C. Oliver (2010) DiLP MAT equation gave the highest an estimate of 22°C, while Royer et al. (2005) DiLP MAT equation gave the lowest estimate of 11°C. The DiLP MAP estimates ranged from 146-240cm/yr. Oliver (2010) DiLP MAP equation gave the lowest estimate, while Peppe et al. (2011) MAP equation gave the highest. The loss ratio for this sub-trial is 35%.

To test an even simpler method, the half leaves described above were carbon-copied and flipped in an attempt to create a reconstructed whole leaf. The leaves

56

processed in this version were "Double Half Royer" as long as the axis was fairly straight and no major amount of area was added. Of the total specimens, 29% were processed as double and 5% were processed as half. These specimens are present in 39 % of the morphotypes. Site averages put into the DiLP MAT equations to get a range of 12-22°C. Oliver (2010) DiLP MAT equation gave the highest estimate of 22°C, while Royer et al. (2005) DiLP MAT equation gave the lowest estimate. When the site averages were put into the DiLP MAP equations the estimates ranged from 147-240 cm/year. Oliver (2010) DiLP MAP equation gave the lowest estimate, while Peppe et al. (2011) MAP equation gave the highest. Loss ratio for this sub-trial is 25%. The time it took to process this sub-trial is about a third less than the "Whole" method took.

-Huff et al. (2003)

Huff et al. (2003) originally conceived of the method on which Royer et al. (2005) based their protocol. The reason for including it is the methodology is simple. It took nearly half the time to use this method when compared to the updated method (i.e. Royer et al. (2005)). The methods applied to Royer: Whole, Half, and Double, are applied to the Huff version (i.e. "Whole Huff", "Half Huff", and "Double Huff"). Because I skipped the damage removal step that Royer et al. (2005) describes, all the leaves presented in this method have zero area loss ratio.

"Whole Huff" has 17% of the specimens being half leaves, which are included in 26% of the morphotypes. When this version's site averages are computed into the DiLP MAT equations the range was 13-26°C. Peppe et al. (2011) DiLP MAT equation gave the

highest, while Royer et al. (2005) was the lowest. The MAP estimate using the DiLP equations ranged 164-240 cm/year. Oliver (2010) DiLP MAP equation gave the lowest estimate, while Peppe et al. (2011) gave the highest estimate.

The "Half Huff" version contains 35% of the specimens being half leaves taken from 43% of the morphotypes. This sub-trial's site averages were put into DiLP MAT equations to get a range of 13-26°C. Peppe et al. (2011) DiLP MAT equation gave the highest, while Royer et al. (2005) was the lowest. Using the site average in the DiLP MAP equations the estimate ranged 163-238cm/year. Oliver (2010) DiLP MAP equation gave the lowest estimate, while Peppe et al. (2011) gave the highest estimate.

"Double Huff", has 29% of the specimens being double of the half leaf and 5% being processed as half leaves. These come from 43% of the morphotypes. When the averages from this version were put in the DiLP MAT equations the range of estimates was 13-26°C. Peppe et al. (2011) DiLP MAT equation gave the highest, while Royer et al. (2005) was the lowest. The DiLP MAP equations gave an estimated range of 164-240 cm/year. Oliver (2010) DiLP MAP equation gave the lowest estimate, while Peppe et al. (2011) gave the highest estimate.

Leaf Area Analysis (LAA)

LAA precipitation estimate was calculated from the averaged leaf area of the 34 specimens' Whole, Half and Doubled Half sub-trials. Because the averaged areas were the same in both methods' Whole, Half and Doubled Half leaf versions, LAA was processed based on the amount of area preserved in each sub-trial. Whole leaf average,

when put into LAA equations, gives estimate range of 144-162 cm/year. The lowest

estimate comes from Wilf et al. (1998) LAA eqution, while the highest comes from

Peppe et al. (2011) equation. Half leaf average, when put into the same equations, to give

a range of 144-163cm/year. The lowest estimate comes from Wilf et al. (1998) LAA

eqution, while the highest comes from Peppe et al. (2011) equation. The Doubled leaf

average area, when put into the LAA equations, gives estimate range of 145-163 cm/year.

The lowest estimate comes from Wilf et al. (1998) LAA eqution, while the highest comes

from Peppe et al. (2011) equation.

VI. DISCUSSION OF METHODOLOGY

Comparing Univariate Methods to the Multivariate Methods for MAT

The paleobotanical methods described above produced a range of paleoclimatic estimates of MAT for the Two Medicine Formation. When comparing the univariate LMA and the multivariate methods, all the LMA equation model estimates are lower than the MAT estimates of CLAMP and DiLP, with the exception of the Royer et al. (2005) LMA equation (Figure 10). Royer et al. (2005) is the outlier possibly due to the fact that there are only two test regions, Eastern US and Panama, and with more leaves being collected at the Panama site (MAT 25°C). In other words it was calibrated using warmer sites. For the most part, multivariate methods produced higher MAT estimates than the LMA. One reason for this is that LMA analysis equations do not incorporate additional features of leaf physiognomy that carry a temperature signal (Wolf, 1993; Huff et al. 2003; Royer et al., 2005; Peppe et al., 2011; Yang et al., 2011).

Other proxies, which seem to agree with these higher temperatures, are marine isotopic temperatures for the late Campanian, like $\delta^{18}O$ from persistent carbonates and Δ_{47} from ammonites. These studies suggest that suggest that MAT was as high as 22-35°C, rather than the 10-12°C estimated by the LMA equations (Upchurch et al., 2015; Dennis et al., 2013; Miller et al., 2013; and references here in). Dennis et al.'s (2013) clumped isotopes give MAT estimates of +22°C from 74 Ma ammonites from the Pierre Shale. Crocodiles were found in Campanian Canada in the Judith River and
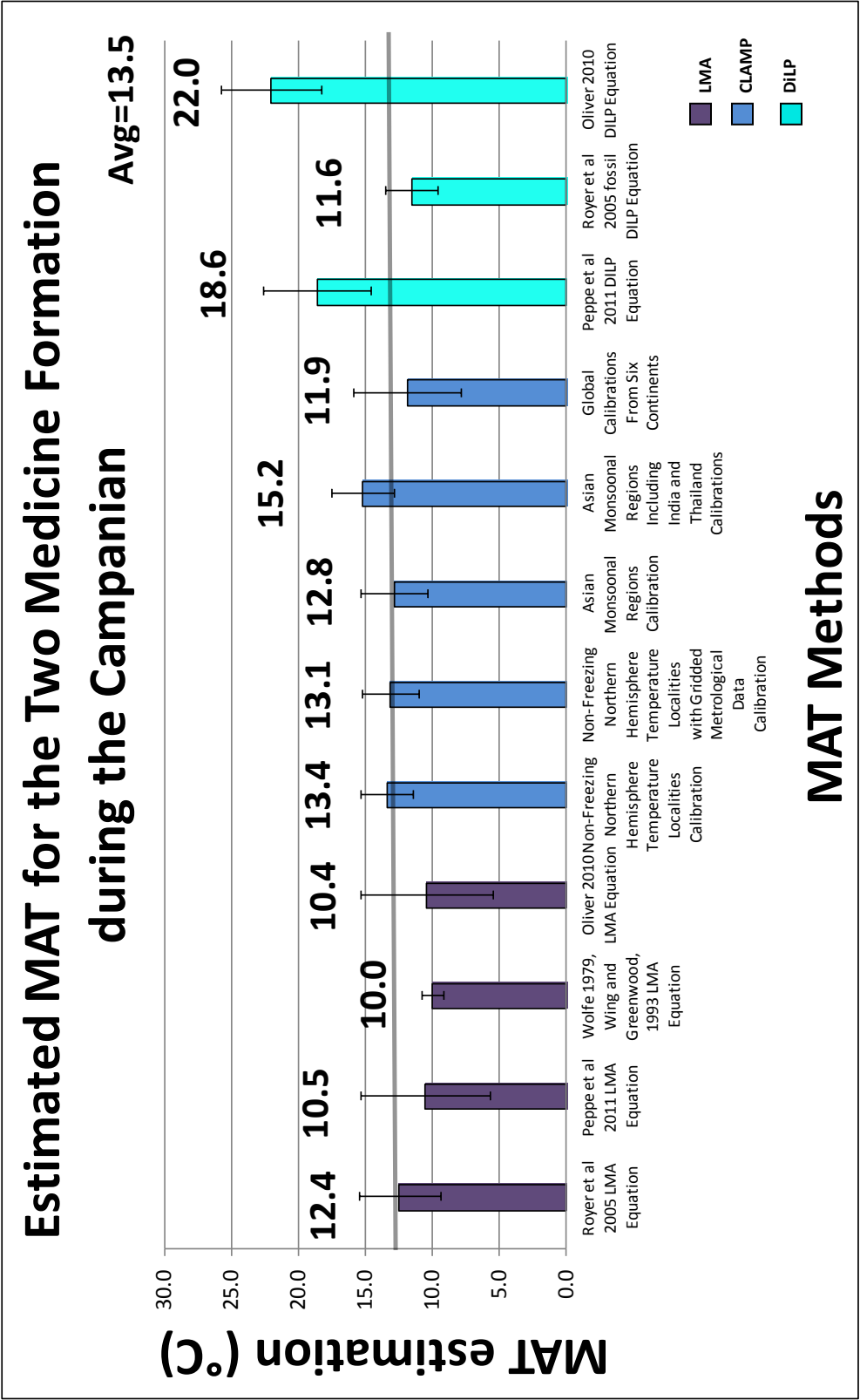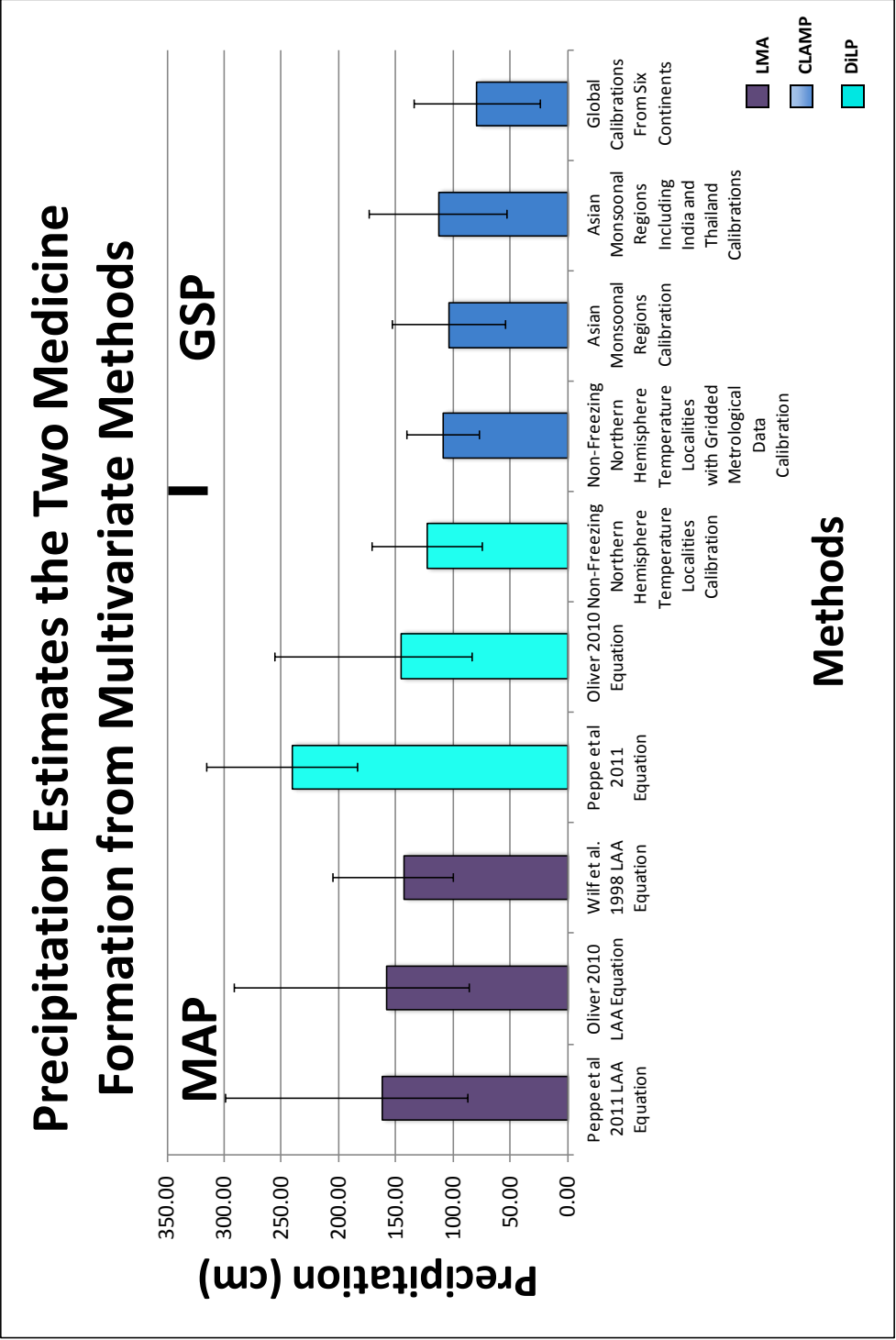
Figure 10. Estimates for MAT across the different methods. The CLAMP calibration region are presenting the averages of the sub-trials for that calibration region. The lowest MAT estiamtes were excluded from the graph.

Dinosaur formations, which means that Campanian Montana is more likely >14°C (Gates et al., 2010; Cullen and Evans, 2016; Markwick, 2007).

Comparing Multivariate Methods for MAT

Comparison of paleoclimate estimates seems to show that DiLP consistently produces higher MAT estimates than CLAMP (Figure 10), with the exception of Royer et al.'s (2005) preliminary DiLP equation that give MAT estimates of ~12°C. Royer et al.'s (2005) DiLP MAT estimate may be small due to the equation only incorporating a small number of sites from two different regions. Other DiLP equations are from numerous global sites as noted in Table 1.

All the sub-trials across all the calibrations of CLAMP demonstrate this lower estimation (Figure 10). There is slight overlap with the uncertainties, but they are on the lower end of the DiLP estimates, and using the average for all the sub-trials, it is lower than DiLP. The CLAMP sub-trial that is closest to the lowest recommended DiLP MAT equation estimate of 19°C, is the Inferred Estimate trial with removal of the smaller of dicot 6,11 and 36 leaves using CLAMP Asian Monsoonal Regions Including India and Thailand, which provided an MAT of 16°C. This sub-trial may be less accurate because only 55% of the categories were coded; the recommended completion is 60% of the categories. The Initial Processing sub-trial allows 68% completion of the categories provides a MAT estimate of 15°C, but the caveat is that we used a modified size, length to width and leaf shape estimates. Still, the estimates from these sub-trials are consistently lower than the DiLP equation estimation of 19°C, which is more congruent

with other fossil localities of similar latitude (Peppe et al. 2011; Yang et al., 2015; Wolfe, 1993; Kennedy et al., 2014; Jacques et al., 2011; Khan et al., 2014; Yang et al., 2011).

Royer et al. (2005) note that CLAMP and LMA are not able to factor out the bias caused by riparian habitats and give erroneously cooler temperature estimates of ~3°C. DiLP is less sensitive to riparian habitats (Royer et al., 2005; Peppe et al., 2011). Lastly, DiLP's MAT estimates are more congruent with the marine geochemical proxy estimates like Dennis et al. (2013) estimate of +22°C (noted above), than those derived from CLAMP. O'Brien et al.'s (2017) work from clumped isotopes for sea surface temperatures in Campanian southern low-middle latitudes estimates MAT to be +16°C.

Comparing Univariate and Multivariate Methods for MAP

The MAP estimates from the lower Two Medicine Formation derived from LAA range from 144-162cm/year, which are lower than Peppe et al. (2011) DiLP MAP estimate of 241 cm/year. Oliver's (2010) DiLP MAP estimate of 147 cm/year is more aligned with the LAA estimates (Figure 11). Both DiLP equations look at different characteristics, which would explain the discrepancy. Because DiLP is still a new method, there is some discussion in the literature about its accuracy in predicting paleoprecipitation (Peppe et al., 2011). Rogers (1990) describes caliche nodules from upper strata of the Two Medicine Formation, which suggests that the region was semi-arid with less than 100cm/year, or at least had extremely high evpotranspiration (Markwick, 2007; Rogers, 1990; Roberts and Kirschbaum, 1995; Mack, 1992). Another consideration why the estimates are low in the univariate methods may be due to the

Figure 11. Estimates for MAP from LMA and DiLP. The CLAMP calibration region are presenting the averages of the sub-trials for that calibration region and show growing season precipitation.

equation being used. These lower estimates, while still higher than 100 cm/year of precipitation for caliche, is comparable to the precipitation estimate for the Maastrichtian Fox Hills Formation of 152cm/year, which is at a similar paleolatitude to the Two Medicine Formation. (Table 2) (Peppe et al., 2011). CLAMP does not provide estimates of MAP like LAA and DiLP, but instead provides estimates of growing season (GSP), which looks at precipitation during months that have no frost, rather than over an entire year. As we see in Figure 11, the GSP is lower than the MAP estimated by LAA and DiLP. CLAMP's GSP error does fall within the range of LAA estimates, but no real comparison can be made without further analysis (Yang et al., 2011; Yang et al., 2015; Wolfe, 1993; Kennedy et al., 2014; Jacques et al., 2011; Khan et al., 2014; Peppe et al., 2011; Royer et al., 2005; Oliver, 2010).

Seasonality and CLAMP

One of the shortcomings with the current form of DiLP is that it can only give estimates for two climate parameters, MAT and MAP. While CLAMP does seem to give non-congruent estimates for MAT and only a partial estimate for MAP, it does pick up seasonality signals in the climate parameters that DiLP cannot. Some the parameters include WMMT and CMMT, which show a very wide gap between the two estimates (Figure 12). WMMT from all the sub-trials and calibration sites ranged from 20-24°C, while the CMMT estimates ranged from 2-9°C. These two estimate ranges would suggest that there is seasonality in with temperature, but these temperature estimates just barely meet the CMMT >5°C threshold of crocodiles and palms (Markwick, 2007). When

comparing the MAT threshold (>13°C) for palms to the MAT estimates from the

CLAMP calibration regions, the most of the MAT estimates do not meet this threshhold

(Table 8) (Markwick, 2007) . Also, when comparing the crocodile threshold of >14°C to

the MAT estimates CLAMP calibration regions, only one calibration region's estimates

meets this threshold (Table 8) (Markwick, 2007). That one calibration region is Asian

Monsoonal Regions Including India and Thailand. The other calibration regions and

global calibration give lower estimates (Figure 12) (Yang et al., 2011; Yang et al., 2015;

Wolfe, 1993; Kennedy et al., 2014; Jacques et al., 2011; Khan et al., 2014; Peppe et al.,

2011; Royer et al., 2005; Oliver, 2010). Until there is more evidence to suggest and agree

with the CLAMP estimates, there likely was not temperature seasonality.

Another seasonality signal from climate parameters estimated by CLAMP is

precipitation during the Three Wet Months and Three Dry Months. When looking at

precipitation during the Three Wet Months, CLAMP gives a range of 53-72 cm, while the

Three Dry Months range give 8-24 cm (Figure 13) (Yang et al., 2011; Yang et al., 2015;

Wolfe, 1993; Kennedy et al., 2014; Jacques et al., 2011; Khan et al., 2014). This is a

large difference in precipitation, and could explain the caliche formation, since there

would a certain period of time of having significantly less rainfall. The lack of rainfall

would also increase the evpotranspiration (Mack, 1992; Markwick, 2007). Seasonality in

precipitation would help explain the severe droughts indicated by hadrosaur death beds

and charcoal beds (Rogers, 1990; Falcon-Lang, 2003; Roberts and Hendrix, 2000). This

type of seasonality, and/or interannual variability in the severity of a dry season, would
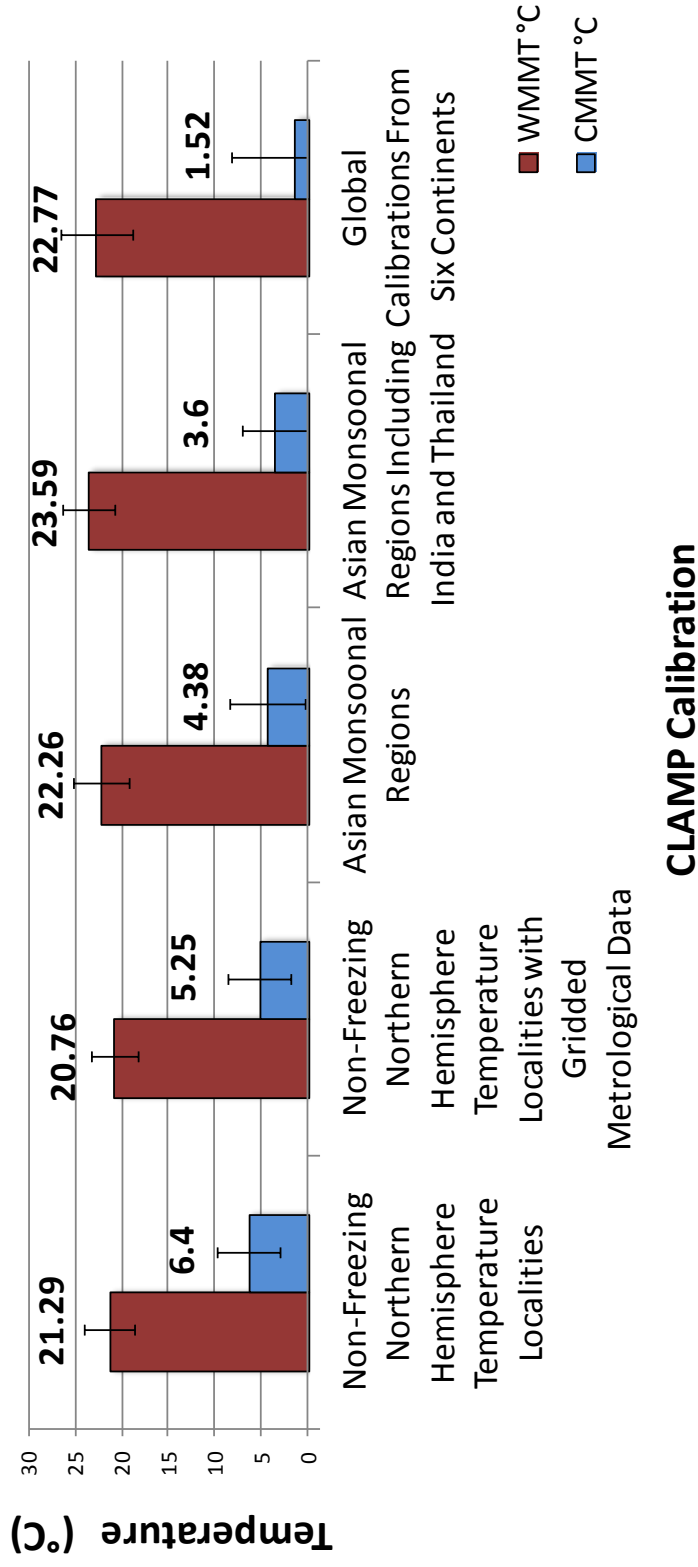
Figure 12. Estimates for warmest month mean temperature and the coldest month mean temperature. The CLAMP calibration region are presenting the averages of the sub-trials for that calibration region.
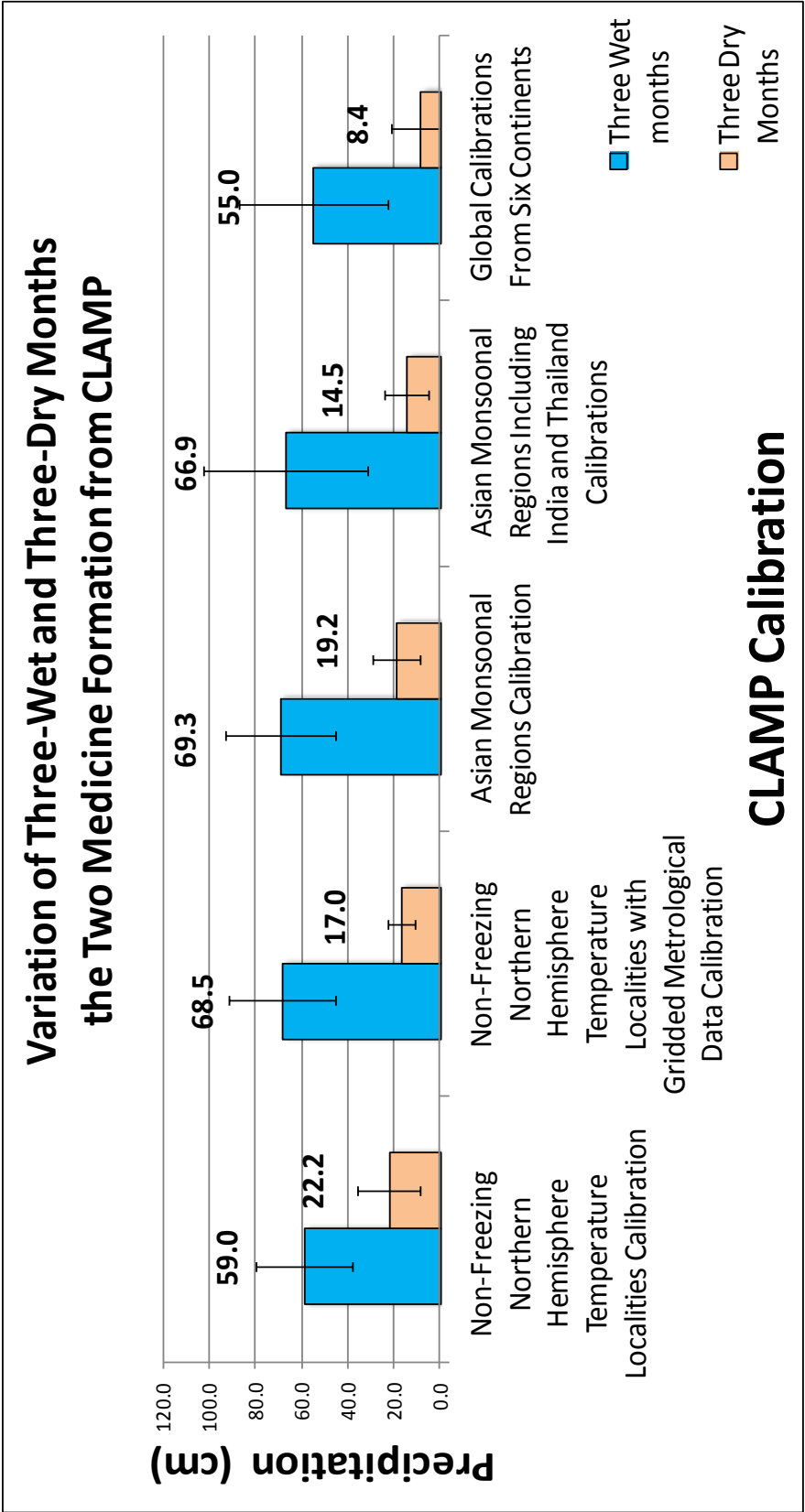
Figure 13. Estimates for precipitation of the three wettest months and three driest months. The CLAMP calibration region are presenting the averages of the sub-trials for that calibration region.

also explain the false annual rings seen in the conifer woods described by Falcon-Lang (2003). With the significant terrestrial evidence that supports these estimates, it is likely that the Two Medicine Formation had precipitation seasonality.

Comparison of CLAMP and DiLP

When comparing speed of processing, CLAMP is the faster method. The catch is that definitions of the categories are correlated with the user's knowledge and training. Each user can look at a leaf at the same time and give potentially different leaf interpretation. As discussed and demonstrated above, how a researcher interprets their fossil flora can greatly alter the paleoclimate estimate. When doing preliminary work using this method, there was a possibility that some of our leaves had spinose teeth due to the images and definitions that CLAMP offered to differentiate it from true teeth. It was only after consulting my advisor and *The Manual of Leaf Architecture* (Conversation with Gary Upchurch; Ellis et al., 2009), that we concluded that the teeth originally categorized as weakly spinose were mucronate with probable glands at the tip, which made us categorize them as true teeth. Categorizing these margins as spinose would have probably increased the temperature estimate.

Different coding of physiognomic traits by different investigators is one of the key reasons for creating DiLP (Wilf et al., 2003; Huff et al. 2003; Royer et al., 2005; Peppe et al. 2011). Also, learning these different codings of physiognomic traits for the CLAMP method can be very hard to an untrained person. The method in identification and being consistent in character definitions becomes even harder with fossil specimens

where ambiguity could take place, which is why CLAMP users need a moderate level of training. This is not an easy method for researchers who do not have previous botanical training.

While CLAMP can estimate seasonality indicating parameters like CMMT and WMMT, Three Wet Months and Three Dry Months (Yang et al., 2011), this study demonstrates that the inconsistencies of coding can affect the climate estimated, but the biggest factor for estimates is the choosing of the calibration regions. Each calibration region, except the Global, is focused of certain climatic characteristics see in the modern world. Choosing the wrong calibration can greatly affect the paleoclimate estimate. Another issue is that even with the uncertainties +/- 2 to 4°C for MAT, the CLAMP method's MAT estimates barely meet the minimum estimate of the recommended DiLP equation of Peppe et al. (2011), which estimated MAT to be 19°C. Even with limited climatic parameter estimates and tedious process, DiLP appears to be the more accurate and congruent plant physiognomic method for estimating paleotemperature.

Sensitivity within Digital Leaf Physiognomy (DiLP)

This study shows that DiLP provides estimates of MAT more in line with other terrestrial proxies and high quality marine geochemical data. The main issue with the current recommended DiLP method is the tedious and time-consuming leaf processing. Another issue is that there is possible valuable information being lost with the damage removal operation. In order to try to mitigate these issues, I decided to test to see if there was any difference between the two methods. Since it was recommended by Huff et al.

(2003) and Dana Royer (personal conversation) not to use Huff et al. (2003) method on fossil leaves, I also tested to see if a modified step of doubling the half leaves in the DiLP process may be effective as well. The site totals for each sub-trial is seen in Table 10, and the subsequent results for each sub-trial are listed in the Table 11 and Table 12.

- Comparing DiLP Methods

When looking at MAT estimates from the two methods, there is very little difference between the two, with the exception of Peppe et al. (2011) equation (Figure 14). This difference may have to do with the fact that the equation uses very different
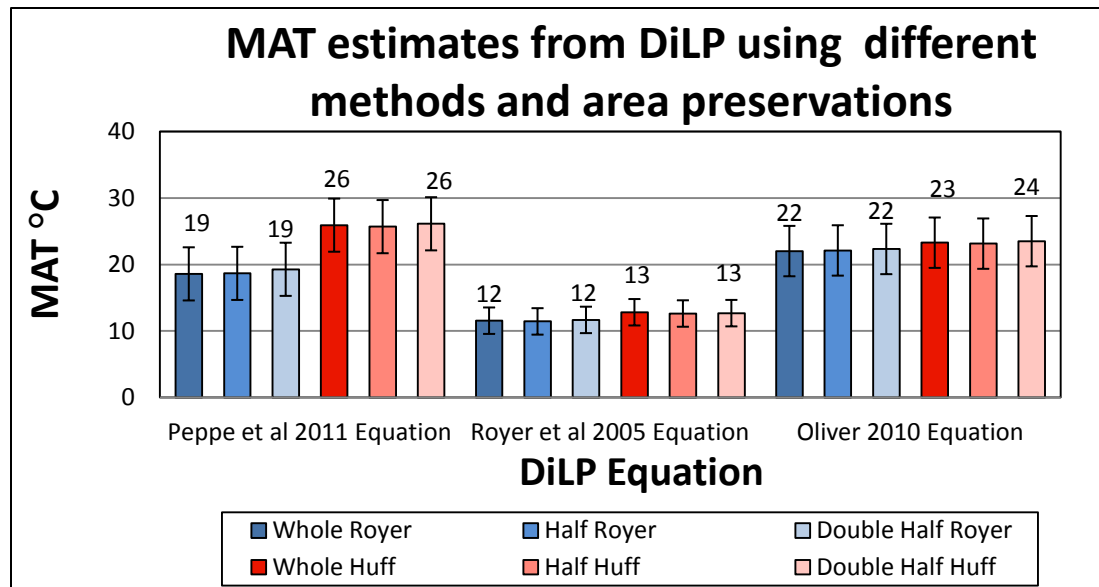
Figure 14. MAT estimates from DiLP using different methods and area preservations. Estimates are shown for Whole Royer, Whole Huff, Double Half Royer, and Double Half Huff.

site mean characteristics (Table 1). For the other DiLP equations, there appears to be little difference between the two methods. These same trends can be seen when look at MAP

estimates as well (Figure 15). There appears to be only a centimeter difference between the two methods of the same preservation area when looking the Peppe et al. (2011) DiLP MAP equation. Oliver (2010) equation shows a slightly higher difference between the two methods, but the standard errors are large and do overlap.
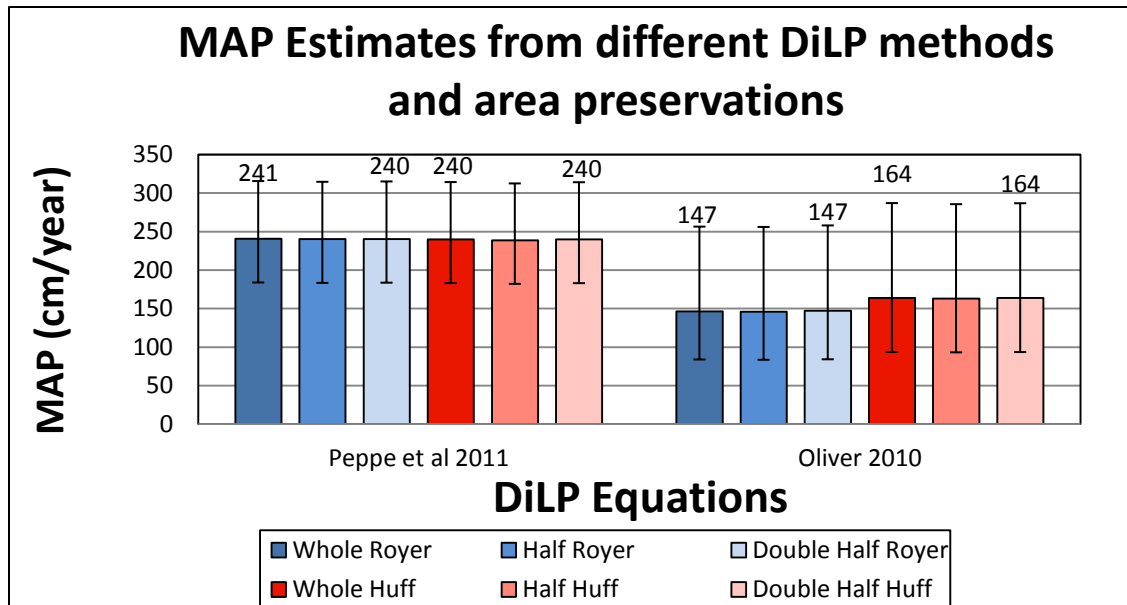
Figure 15. MAP estimates from different DiLP methods and area preservations. Estimates are shown for Whole Royer, Whole Huff, Double Half Royer, and Double Half Huff.

These results are promising because the Huff et al. (2003) method took half the processing time as Royer et al. (2005). The speed, as discussed early, is due to skipping the operation to remove damage. In Royer et al. (2005), this operation was done to select pristine margins with its subsequent blade area that would yield more accurate results. What my test shows is that the meticulous detail of selecting pristine margins may not be warranted when looking at MAT.

-Area of Preservation

Another comparative test that I did was see how different preservation areas affected the outcome of the estimates. The goal of this test was to see if doubling half leaf, which saves time, would give similar results. Judging by the results shwn in Figure 14 and Figure 15, there is little difference between using a whole leaf, half leaf or double half leaf. This trend is seen in both Royer et al. (2005) method and Huff et al. (2003) method. As a preliminary result, it shows that double half leaves, when possible, has no effect on the final outcome. More research is needed, because a majority of the leaves processed in each sub-trial were still whole leaves: with "Whole Royer" and "Whole Huff ," only 17% of the leaves were half leaves, while with "Double Royer" and "Double Huff " only 29% of the leaves were double halves. Another possible issue with using double half leaves is the introduction of errors associated with area gain. Still, results are promising.

-Calibration Equations

The choice of calibration equation seems to have the greatest effect on estimated MAT and MAP. This is exemplified by Royer et al. (2005) DiLP MAT equation. As stated in previous parts, the reason may be due to too few modern day calibration sites being used. Another issue is that each equation also looks at different averaged site leaf parameters, which could potentially have a major effect on the final climate estimation. This is seen in the difference between Peppe et al. (2011) DiLP MAP equation and Oliver

(2010) DiLP MAP equation. Each calibration had near the same number of regions and calibrations, yet produced very different estimates. When looking at each equation, they used different site averaged leaf parameters. Oliver (2010) DiLP MAP estimates were similar to LAA estimates, which I argue as being the better method of estimating paleoprecipitation. For DiLP MAP equations, the equations are based on LAA (see Table 1), where it is a known issue that it over estimates on MAP (Peppe et al. 2011). These issues maybe possibly carried over to the DiLP equations.

While these results are promising, more research is needed. DiLP has great potential in estimating paleoclimate, but the time consumption of the process is a major downside. The preliminary results I have presented should be helpful in future studies.

VII. DISCUSSION ON THE PALEOCLIMATE OF

THE TWO MEDICINE FORMATION

Mean Annual Temperature (MAT)

The main goal of the study was to identify the paleoclimate of the Two Medicine Formation from paleobotanical proxies. As was discussed in the previous sections, univariate and multivariate methods were both used in this study. The univariate method LMA gives cooler MAT estimate range of 8-12°C. This counters the terrestrial evidence of palms that was found by Crabtree (1987b). Again, palms require a MAT of >13°C, therefore LMA is not a reliable method for paleoclimate for the Two Medicine Formation.

Another terrestrial line of evidence that contradicts the LMA MAT estimates is the presence of crocodiles or crocodilomorphs. They occur in the slightly younger (76-74Ma) Montana Judith River and Canadian Dinosaur Formation (Gates et al., 2010). Crocodilomorphs have been used as a paleontological climate proxy to provide a minimum CMMT of 5°C and have a minimum MAT of 14 to 16°C (Gates et al., 2010; Markwick, 1996, 2007). Even though these crocodilomorph fossils are younger and come from a slightly higher in section formations, the suggestive idea is that the lower Two Medicine Formation was just as warm, or warmer, than what the crocodilomorph fossils are giving us. This conclusion is based on the temperature gradient of 0.4°C/ degree latitude proposed by Upchurch et al. (2015) for the late Campanian to Maastrichtian. It is similar to latitudinal temperature gradients proposed for other periods of warm climate

such as the Eocene (Upchurch et al., 2015). Therefore, LMA is unreliable for estimating MAT for the Two Medicine Formation.

The multivariate methods of CLAMP and DiLP used in this study were more congruent with agreeable to the MAT temperature estimates based on palm and crocodiles. Of the multivariate methods tested, DiLP was the better of the two methods because its estimates were warmer and in better agreement with the other proxies. While CLAMP, with the inclusion of its uncertainties, does fall within the range of temperature estimates of DiLP, palm fossils, and crocodilians, there is no indication that the estimated temperatures from CLAMP could be higher and be within the range of other proxies that give MAT estimates of 16-22+°C, such as stable isotopes (discussed later) (O'Brien, 2017; Dennis et al., 2013). The cooler temperatures of CLAMP are a known issue and therefore caution should be used when using CLAMP and is my reasoning for DiLP is probably the more accurate multivariate method for MAT (Yang, et al. 2011; Peppe et al., 2011; Oliver, 2010; Huff et al., 2003)

Peppe et al.'s (2011) DiLP equation gives a MAT of 19°C, while Oliver's (2010) equation gives an estimate of 22°C. Using these estimates, and the fact they align with the southern low-middle latitudes isotope sea surface MAT temperature +16°C of O'Brien et al. (2017) and estimates of +22°C of Dennis et al. (2013), the ~80Ma fossil leaves of the lower Two Medicine Formation give a mean annual temperature of 19-22°C. These estimates concur with the fossil palms that was found by Crabtree (1987a,1987b), as well as the crocodile fossils found in Canada, indicating that the MAT must be at least 14°C (Gates et al., 2010; Markwick, 1996, 2007). As stated earlier, the absolute lowest a palm and crocodile can tolerate is 5°C CMMT, with maybe only a few

hours of colder temps (Gates et al., 2010; Markwick, 1996, 2007; Manchester et al., 2010; Greenwood and Wing, 1995).

As it was previously mentioned, the DiLP temperature estimates are similar to the estimates from paleogeochemical proxies. Late Campanian (~74 Ma) clumped isotopes of $\delta^{18}O_w$, $\delta^{13}O_c$, and Δ_{47} off of unaltered ammonite shells from the Western Interior Seaway gives temperature estimates ~22°C (Dennis et al., 2013), with the assumption of the globe being ice free (Petersen et al., 2016). Other clumped isotope studies do give cooler temps that are similar to LMA estimates of 10-12°C, as well as warmer temps that do not concur with paleobotanical estimates, but all have noted caution due to the variable conditions that the Western Interior Seaway can have in salinity, fresh water input, and others (Petersen et al., 2016; Peppe et al., 2011; Dennis et al., 2013).

Because we cannot receive reliable estimates from clumped isotopes, the paleogeochemical proxy TEX_{86} marine temperatures for middle latitudes were used. TEX_{86} comes from 86 carbons aligned lipids of single celled water organisms that proliferate when temperatures are warm, so it is strongly correlated to sea surface temperatures (Upchurch et al., 2015; O'Brien et al., 2017). While O'Brien et al. (2017) inconveniently has a gap for ~80 Ma middle Campanian, but they do provide trends of the TEX_{86} where sea surface temperature estimates could be extrapolated. When combining this extrapolation with bottom ocean water $\delta^{18}O_b$ taken from the equivalent southern latitude, O'Brien et al. (2017) conclude that MAT at the south low to middle latitudes ocean surface during the time of the middle Campanian was ~19-21°C. This is almost the exact same range, 19-22°C that I received using the two different DiLP MAT equations (e.g. Oliver, 2010; Peppe et al. 2011).

Mean Annual Precipitation (MAP)

Since CLAMP does not calculate MAP, LAA and DiLP were used (Yang et al.,2011). The lowest estimate for MAP is needed due to the known issue of MAP estimates being too high from leaf physiognomy (Peppe et al., 2011). In general, the LAA equations seem to give the lowest estimate for MAP. The lowest estimate comes from Wilf et al.' (1998) LAA equation, 144cm/year, but Oliver (2010) DiLP equation yields the next lowest estimate of 147cm/year, which is comparable to the other LAA equations. Wilf et al.'s (1998) LAA equation and Oliver's (2010) DiLP equation are fairly comparable to each other, and are probably the better equations to estimate MAP. The LAA estimate is ~150 cm/year. Using these estimates, I suggest that the ~80 Ma fossil leaves of the lower Two Medicine Formation gives a mean annual precipitation range of roughly ~150 cm/year.

This MAP range is congruent with the other paleoclimate proxies, such as the crocodilomorph fossils which requires a minimum of 500 mm (Markwick, 1996, 2007). The caveat is that the crocodilomorphs are found in the Judith River Formation, where it was likely that standing water could be found, since the formation is coastal facies, whereas the Two Medicine Formation is alluvial (river) faceis (Markwick, 1996, 2007; Gates et al., 2010; Cullen and Evans, 2016). This sedimentology description indicates that there was running water at times (Crabtree, 1987b; Rogers, 1990).

Another sedimentolgical feature that appears to disagree with the MAP estimate of ~150 cm/year is the series of caliche nodule horizons that were found with Hadrosauridae (duckbilled dinosaur) fossils (Rogers, 1990). Today, caliche forms in

drought prone environments where MAP is less than 100cm/yr (Buck and Mack, 1995; Mack, 1992). Markwick (2007) makes note that caliche and other carbonate-based soils can form in areas with higher MAP if the parent material is of calcareous origin (Figure 16). The Two Medicine Formation has no indication of calcarious parent material.
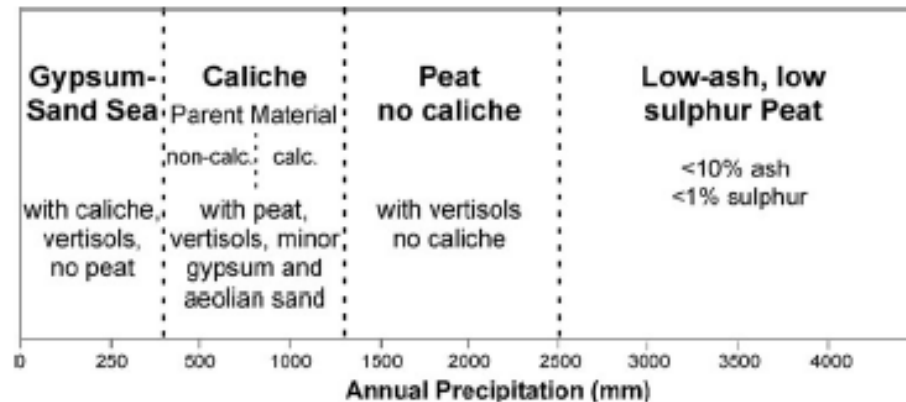
Figure 16. Carbonate parent material may cause caliche to form in precipitation greater than 100 cm/year. This image is taken from Markwick (2007) that details the work of Gyllenhaal (1991).

Yet, one of the main requirements for caliche nodules to form is that evapotranspiration exceeds precipitation (Mack 1992; Markwick, 2007), which occurs in arid, semi-arid, and sub-humid environments (Mack, 1992; Buck and Mack, 1995).

Using this information, the evidence from this particular site suggests is that the climate may have been on the cusp of two climate regimes, where it shifted from wet to dry. Looking at Figure 16, my MAP estimate of ~150 cm/yr does not fall within the cusp of having caliche. Yet, Rogers' (1990) Two Medicine Formation's sedimentology describes varying layers of caliche, but with no known coal or peat layers even though fresh water gastropods were found (Falcon-Lang, 2003; Crabtree, 1987b). There are,

however, layers of charcoal, which indicate dry events (Roberts and Hendrix, 2000). Combined, these layers could be an indication of seasonality (Rogers 1990) or strong variability on interannual to millennial time scales possibly associated with the rise and fall of the Western Interior Seaway (e.g. Haq, 2014), but will not be discussed further here.

Paleoseasonality

Growth rings in fossil wood reinforce the case for drought during a dry season, based on analysis of the fossilized forests near Choteau, Montana (Rogers et al., 1993; Falcon-Lang, 2003; Roberts and Hendrix, 2000). Falcon-Lang's (2003) analysis of fossil conifer wood determined that there was growth interruption, but no consistent annual rings to indicate strong temperature seasonality. These types of interruptions are commonly seen in modern tropical climates, where temperatures are consistently above freezing. Like in the previous caliche example, the wood anatomy is exemplifying a highly variable environment, and recording unexpected drought events that could carry on for months at a time (Falcon-Lang, 2003). Falcon-Lang (2003) also makes note of true annual rings seen in woods that are from slightly higher paleolatitudes (e.g. greater than 55°). There is definitely some sort of seasonality, but temperature does not appears to be the cause.

This lack of strong temperature is in conflict with CLAMP climate parameters of cold month (CMMT) and warm month mean temperatures (WMMT). When looking at Crabtree (1987b) leaves through CLAMP, there is a clear indication of paleoseasonality.

Across all the calibration data sets and sub-trials, WMMT are between 20-24°C while the CMMT are between 2-8°C, which indicates a Mean Annual Range of Temperature (MART) of 14 to 20°C. The lower estimates of MART are not congruent with the palms and crocodiles. The CMMT of 5°C is the lowest that crocodilomorphs and palms can survive (Markwick, 2007). Markwick (2007) does note that the lower thresholds of these two proxies may have evolved due to human selection.

The presence caliche in conjunction with the sedimentology and fossils indicate possible seasonal precipitation. This is in agreement with seasonality signal from CLAMP's Three Wet Months precipitation and Three Dry Months precipitation. CLAMP's estimates from Three Wet Months, 53-72 cm, and Three Dry Months, 8-24cm, would likely cause an increase in the evpatranspiration, which is needed to create caliche (Mack, 1992; Markwick, 2007). The hadrosaur death beds and charcoal beds, which were caused by severe drought events, are probably related to precipitation seasonality (Rogers, 1990; Falcon-Lang, 2003; Roberts and Hendrix, 2000). This precipitation seasonality is also in agreement with Fricke et al. (2010) computer model-isotope work for Western Interior Campanian. This work indicates that there was significant rainfall during certain times of the year and significantly less rainfall during other parts of the year for the Campanian of higher latitudes, including the Two Medicine Formation (Fricke et al., 2010). These shifts in rain are thought to be monsoonal, which coincidently maybe being picked up by CLAMP's calibration region "Asian Monsoonal Regions Including India and Thailand." This is the calibration that provides temperature estimates most congruent with the other proxies (Fricke et al., 2010; Yang et al., 2011; Jacques et al., 2011; Khan et al., 2014).

Climate Classification

From Crabtree's (1987b) dicot leaves and the supporting proxy estimates, the

lower Two Medicine Formation had a MAT of 19-22°C with a MAP of ~150cm/year.

These estimates can be used to fit the Two Medicine Formation within a regional climatic

classification. Two commonly used climate classification systems are the Köppen

Classification and the Holdridge Life Zone Classification (Holdridge, 1967; Rohli and

Vega, 2015). Both systems take into account the main vegetation types and relate them to

different climate parameters (Rohli and Vega, 2015; Aguado and Burt, 2004).

Using the Köppen Classification, middle Campanian of the Two Medicine Formation

most likely had a CMMT of >5°C as indicated by the palms and crocodiles. This is

between 0°C and 18°C CMMT, that characterizes C climates, or Mesothermal/Temperate

(Rohli and Vega, 2015; Aguado and Burt, 2004). Mesothermal/Temperate classification

is consistent with the Two Medicine Formation MAT estimate of 19-22°C. Another

classification distinguisher is Cfa, which means there has to be constant rainfall with little

to dry season and the hottest month has to be greater than 22°C (Rohli and Vega, 2015).

This is exemplified by the MAT estimate being around 22°C and by CLAMP's warmest

WMMT estimates of 20°C. CLAMP's Three Wet Months and Three Dry Months

estimates indicate year round, but seasonal, rainfall. Today's regions with these

classifications are found in southeast Asia/northern India, southeastern United States, and

southern Brazil/Argentina (Figure 17) (Rohli and Vega, 2015; Aguado and Burt, 2004;

Kottek et al.,2006).
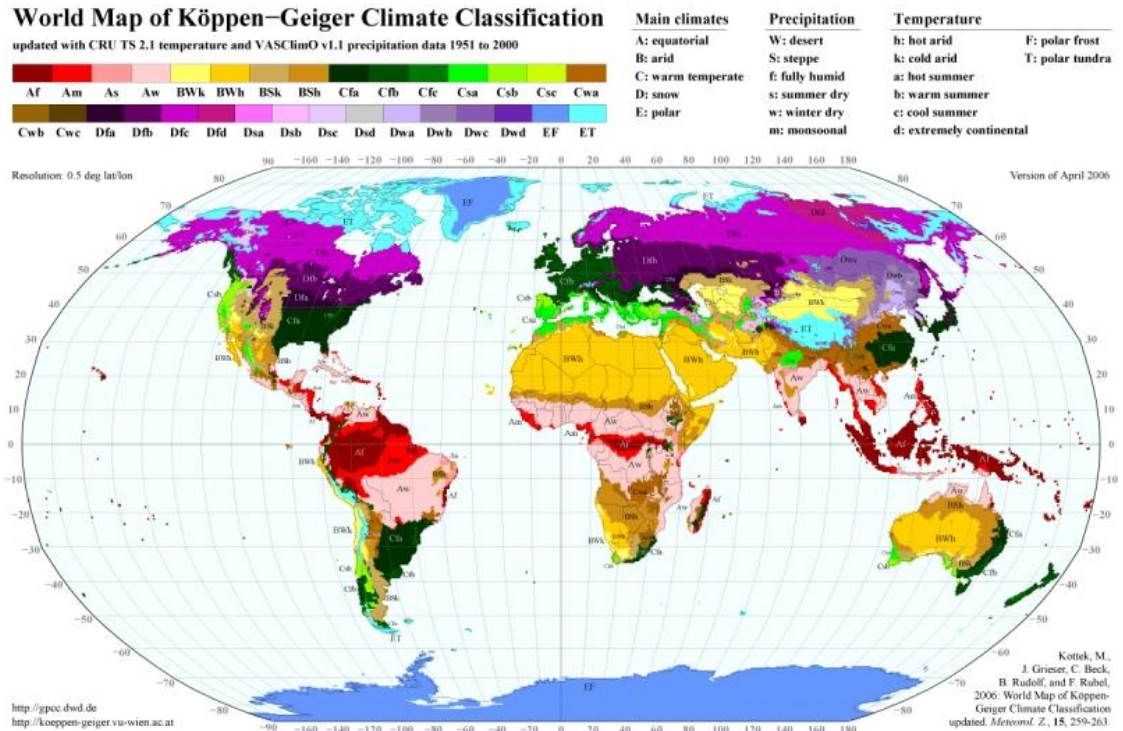
Figure 17. World distribution for Köppen-Geiger climate classification. Taken from the work of Kottek et al. (2006).

The Holdridge Life Zone Classification is used to assist ecologists in the classification of climate and vegetation, with the focus being more on the latter's temperature limits (Holdridge, 1967). It has since become the more useful tool in understanding tropical climates (Rohli and Vega, 2015). Figure 18 shows all the climate regimes in Holdridge's Classification and a critical temperature line of ≤16°C (Schimel,2013; Holdridge, 1967). Using the estimates for MAT (19-22°C) and MAP (~150cm/year) that I obtained for the lower Two Medicine Formation, I determine what the possible life zone was ~80 Ma. By looking at Figure 18, and inserting my estimates I obtain a life Moist Forest (indicated by the blue star). The regime is Moist Forest. This

regime is in agreement with the previously described proxies like palm and crocodiles.

The lower Two Medicine Formation of ~80 Ma was most likely Subtropical and Sub-

humid to humid, which is agreeable to the Köppen Classification.
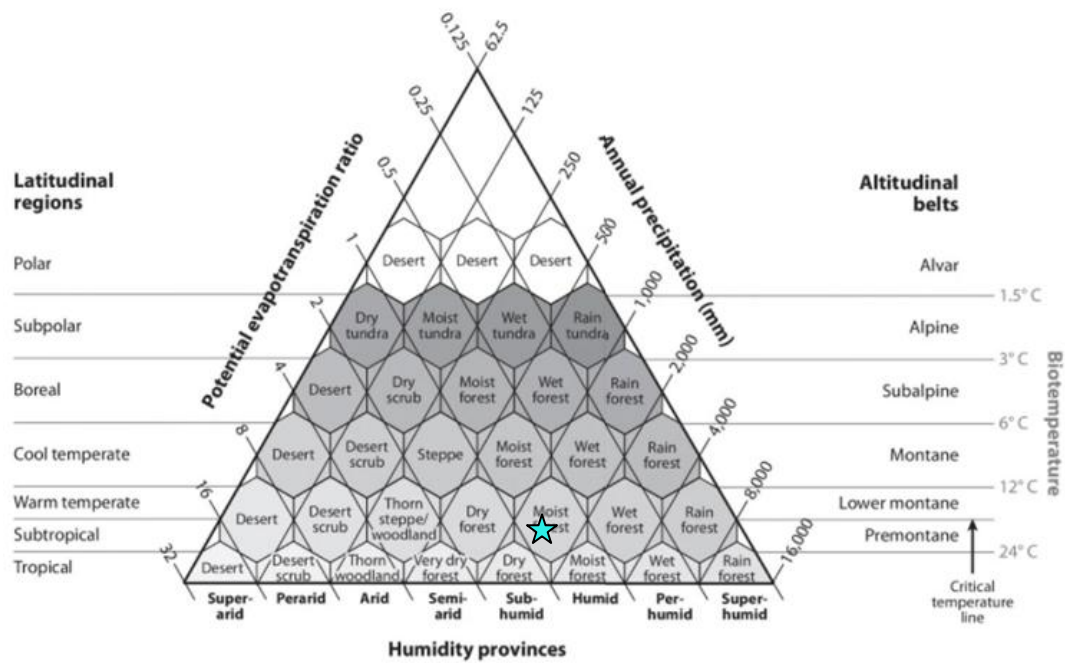
Figure 18. The Two Medicine Formation categorizes as Moist Forest in the
Holdridge Life Zone. Holdridge Life Zone (1967) as sourced from "Climate and
Ecosystem" (Schimel,2013).

VIII. CONCLUSION

When Crabtree (1987b) presented his dissertation there were few tools that could be used to interpret ancient terrestrial climates from leaf physiognomy other than LMA. Since that time, several methods of leaf analysis have been developed to reconstruct paleoclimate from leaf physiognomy. Current methods include univariate methods, LMA and LAA, and multivariate methods, CLAMP and DiLP. One goal of this study was to determine the degree of congruence between the different methods. It was found that the univariate Leaf margin analysis (LMA) gave consistently lower mean annual temperature (MAT) estimates than the multivariates, CLAMP and DiLP. Leaf area analysis (LAA) gave comparable MAP to Oliver's (2010) DiLP equation for MAP. The other DiLP MAP estimates gave very high estimates, so it may appear that LAA is, at least in this case, the better method to estimate MAP.

When looking at MAT estimates between the two multivariate methods, CLAMP gives consistently cooler temperatures than DiLP. This was expected since CLAMP relies heavily on LMA, and it is a known issue for the method. DiLP gives consistently warmer temperatures that are in agreement with the other climate proxies of crocodilomorphs and geochemistry. While CLAMP's uncertainties in the MAT could be on par with DiLP, the other climate parameters are not in agreement with the other proxies like crocodilomorphs and palms. CLAMP's estimated CMMT is at or just above the minimum 5°C threshold of what is seen in today's crocodilomorphs and palms (Markwick, 2007). While it possible that Two Medicine had that minimum CMMT, it seems unlikely. The suggestion of warmer temperatures is indicated from isotope work

and the presence of false annual rings preserved conifer woods taken from the Two

Medicine Formation (Falcon-Lang, 2003). These false annual rings have been

interpreted to be the result of drought events, rather than cold temperatures.

While the multivariate method CLAMP provides detailed and useful

paleoclimatic information on seasonality, its MAT estimates are not as reliable as DiLP,

and it does not estimate MAP. As this study has shown, this approach can generate

inconsistent temperature estimates due to various researchers' interpretations of leaf

parameters. Also, the estimates for MAT are low relative to other proxies, which puts the

other parameters into question. One similar study to mine was performed in Europe by

Thiel et al., (2012). They concluded that univariate methods and CLAMP gave

anomalously low MAT values when compared to the Coexistence method, a method that

uses modern species climate regimes to infer the paleoclimate of nearest relative (not

used in this study), when looking at Late Pliocene floras of Europe (Thiel et al., 2012).

Valuable information can be obtained from both CLAMP and DiLP, but other proxy

estimates need to be taken into consideration to get a more robust and detailed

paleoclimatic reconstruction.

Another implication of this study is to improve estimations of the mean annual

temperature and mean annual precipitation of the environment of the Two Medicine

Formation. From the Peppe et al. (2011) DiLP MAT equation suggests a warm

temperature of 19°C, while the Oliver (2010) DiLP MAT equation gives a slightly

warmer 22°C. Therefore, a mean annual temperature between 19-22°C is suggested for

the lower Two Medicine Formation. The paleotemperature estimate is congruent with

marine geochemical data from similar latitudes, and fits the temperature thresholds for crocodilomorphs and palms.

My precipitation estimate for the Two Medicine formation may be the first reported estimate in the paleoclimate literature. Mean annual precipitation, when looking at Wilf et al. (1998) Leaf area analysis equation, the estimate is 144cm/year. This estimate is similar to Oliver's (2010) DiLP MAP equation that yields a yearly precipitation estimate of 147cm/yr. Because these two MAP estimates are very similar to teach other and the other LAA estimates, and fall within one standard error of each other, I propose that the lower Two Medicine Formation had a mean annual precipitation of ~150cm/year. The precipitation estimate of ~150cm/year may still be high too due to the known issue of LAA estimating high for MAP and reflect a compounding effect of MAT and MAP that was noted by Peppe et al. (2011).

Another line of evidence that supports a lower estimate is the presence of caliche, which typically indicates less than 100 cm/yr of precipitation. This low precipitation typically reflects very high evapotranspiration to create dry conditions, which is needed to form caliche (Markwick (2007). As it was shown in Markwick (2007), this 100 cm/yr is not always the case, especially if the parent material has high calcium carbonate content. From Markwick (2007), if there is parent material, caliche could be formed with MAP amounts <150cm/yr. My precipitation estimate is right on the boundary of being able to develop caliche or not, using Markwick (2007). Since caliche was found in several different strata of the Two Medicine Formation, and there is no indication of calcareous parent material, all evidence suggests the MAP is lower than 150cm/year. The

caviot is that caliche is found stratigrahically higher than the leaf beds, which could be a drying trend during the Campanian for the region.

These layers of caliche may be indicative of paleoseasonality. The DiLP methods cannot provide evidence of this, and the CLAMP CMMT temperatures is too cold, and not reflected in the fossil record. However, when looking at CLAMP's Three Wet Months Three and Three Dry Months estimates, there is a clear possibility of the Two Medicine Formation having precipitation seasonality. Seasonality of precipitation is what causes caliche to form due to high evapotranspiration during the dry season. Other fossils such as charcoal and the hadrosaur deathbeds, seem to agree with this interpretation, as these occured during drought events.

When imputing the estimated climate parameters into the Köppen Classification and the Holdridge Life Zone Classification, the subsequent climate regimes predict minor seasonality of wet to dry. The regime for Köppen Classification was mesothermal/temperate, that has year-round rainfall with little to no dry season, and warm temperatures (Cfa). For the Holdridge Life Zone, the Two Medicine Formation has a climate characteristic of Moist Subtropical Forest. With this information, the lower Two Medicine Formation had a warm Mean Annual Temperature of climate ~20°C that was fairly humid, and had precipitation seasonality.

Another goal was to determine a faster and more effective method to determine climate from fossil leaves. While this study did not find the fastest and most reliable method, it suggests that DiLP is most congruent with other paleoclimate proxies such as high-quality oxygen isotope data. Even though, DiLP may be the most effective paleoclimate proxy, it is also the most time-consuming method. I introduce a modified

technique of doubling the better-preserved half of the leaf with Adobe Photoshop Elements 7.0 (Adobe Systems, San Jose, California, USA) decreases the time needed to process the leaf features. While this step of doubling the better half needs to be further tested, the estimates from this modified technique are on par with the estimates for the whole leaves. Doing this modified technique may lead to improvements in processing speed.

In conclusion, this study provides a more refined reconstruction of climate for the Upper Cretaceous Two Medicine Formation. This updated data should be valuable to paleoclimatologists who are trying to reconstruct climate on a continental and global scale and test the output of atmospheric general circulation models (e.g. Upchurch et al., 2015; Upchurch et al., 2007). The study may also be useful for paleontologists trying to reconstruct paleoenvironments for the dinosaurs (Chin, 2007; Retallack, 1997). More work and improvement need to be done in order to refine the paleoclimate estimates from paleobotanical means. I am hoping my work may influence others in the field that paleoclimatological studies are needed to better understand how the world that we live in works and changes through time.
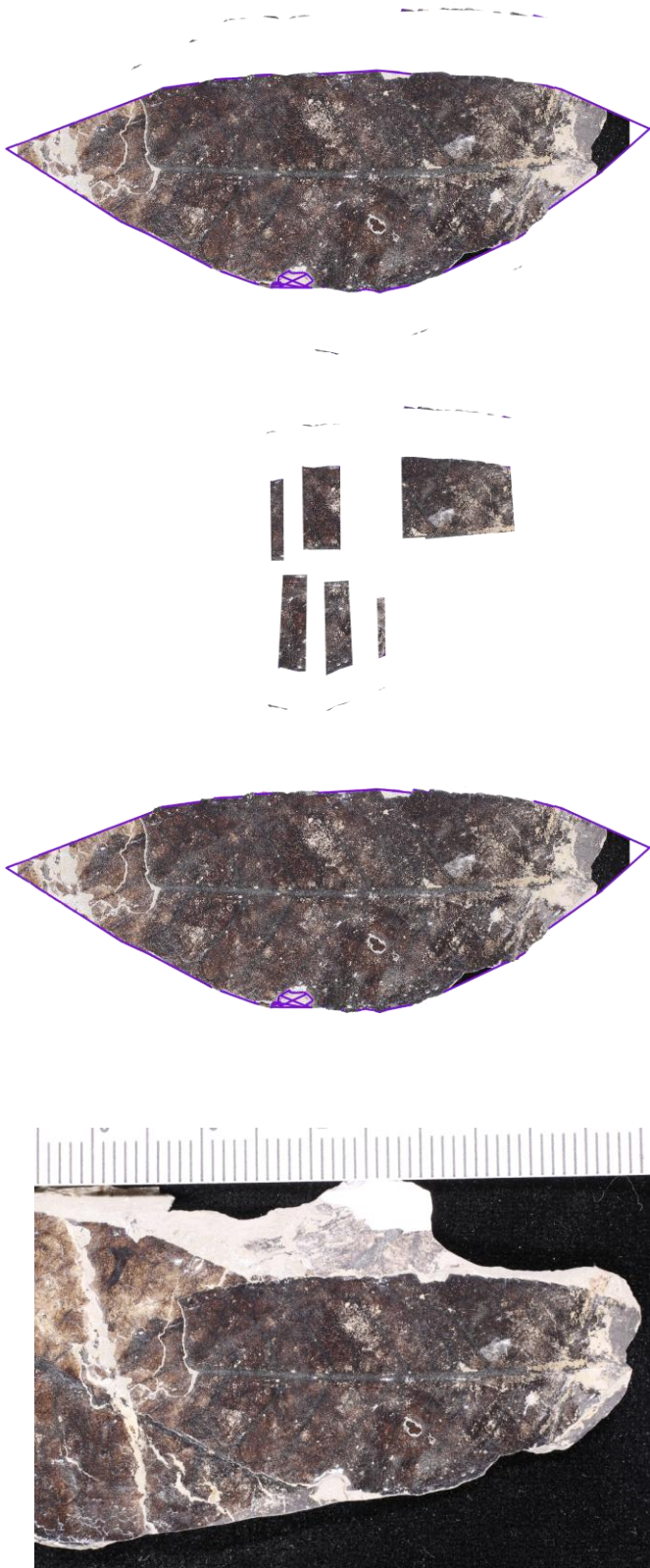
Huff et al. (2003)
Method

Royer et al. (2005)
Method

Specimen out of rock

Illustration 1. Dicot 1 27A/01/004 (A)

Specimen is entire margined
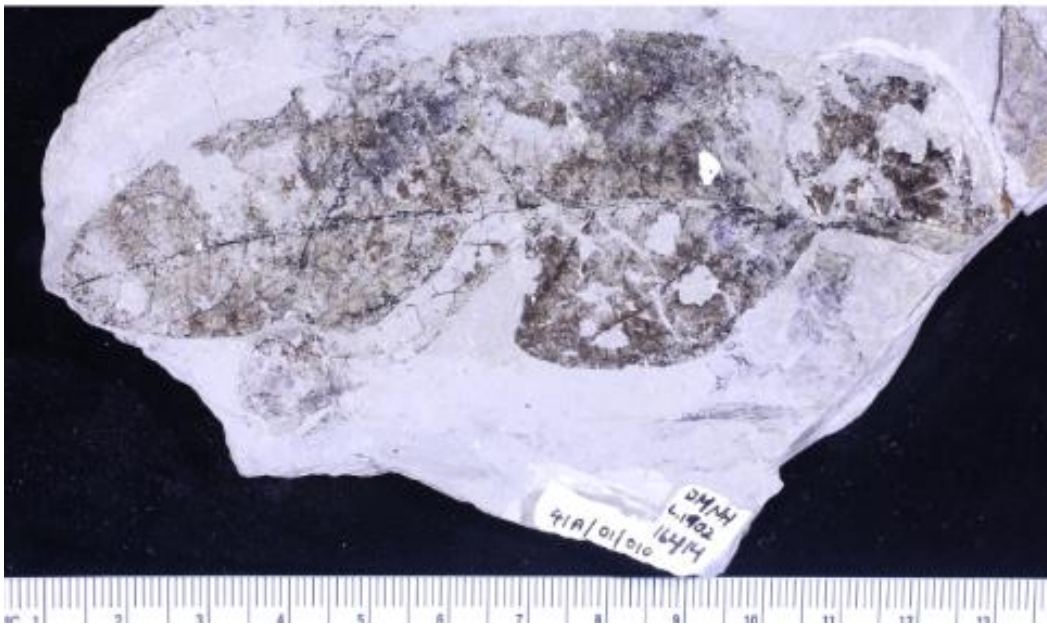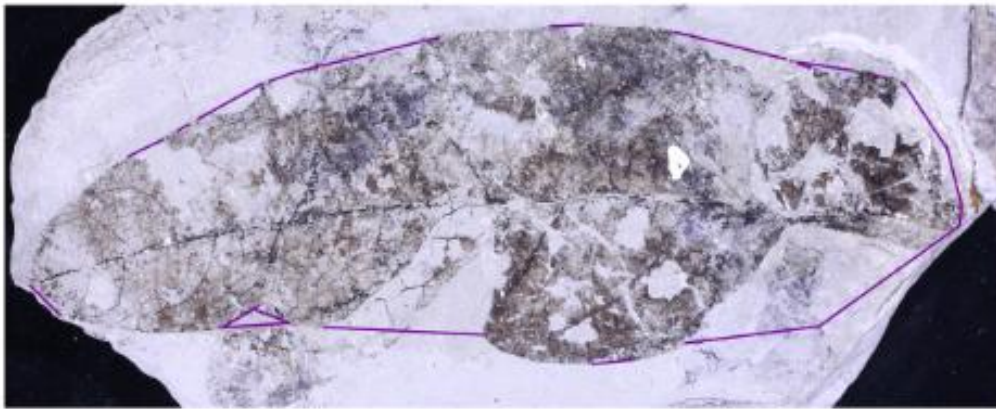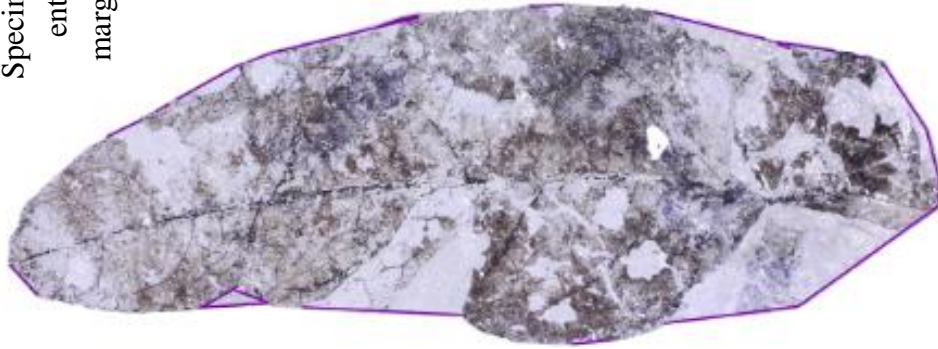
Illustration 2. Dicot 1 16414

Huff et al. (2003)
Method

Royer et al. (2005)
Method

Specimen out of rock
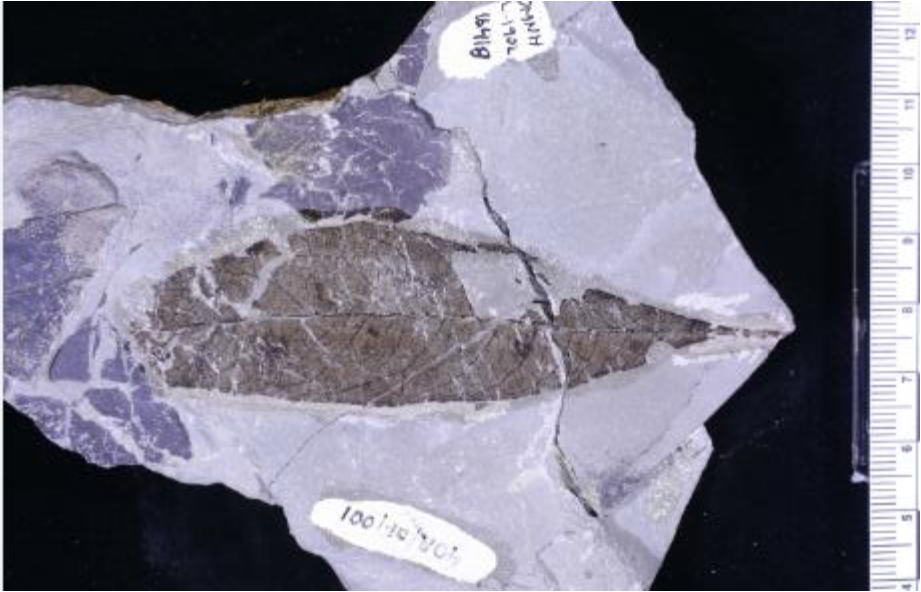
Illustration 3. Dicot 1 16418

Specimen is entire margined

Illustration 4. Dicot 3 39A/03/002

Illustration 5. Dicot 04 16368 (002)

Specimen out of rock

Royer et al. (2005) Method

Huff et al. (2003) Method

Whole   Half   Double Half
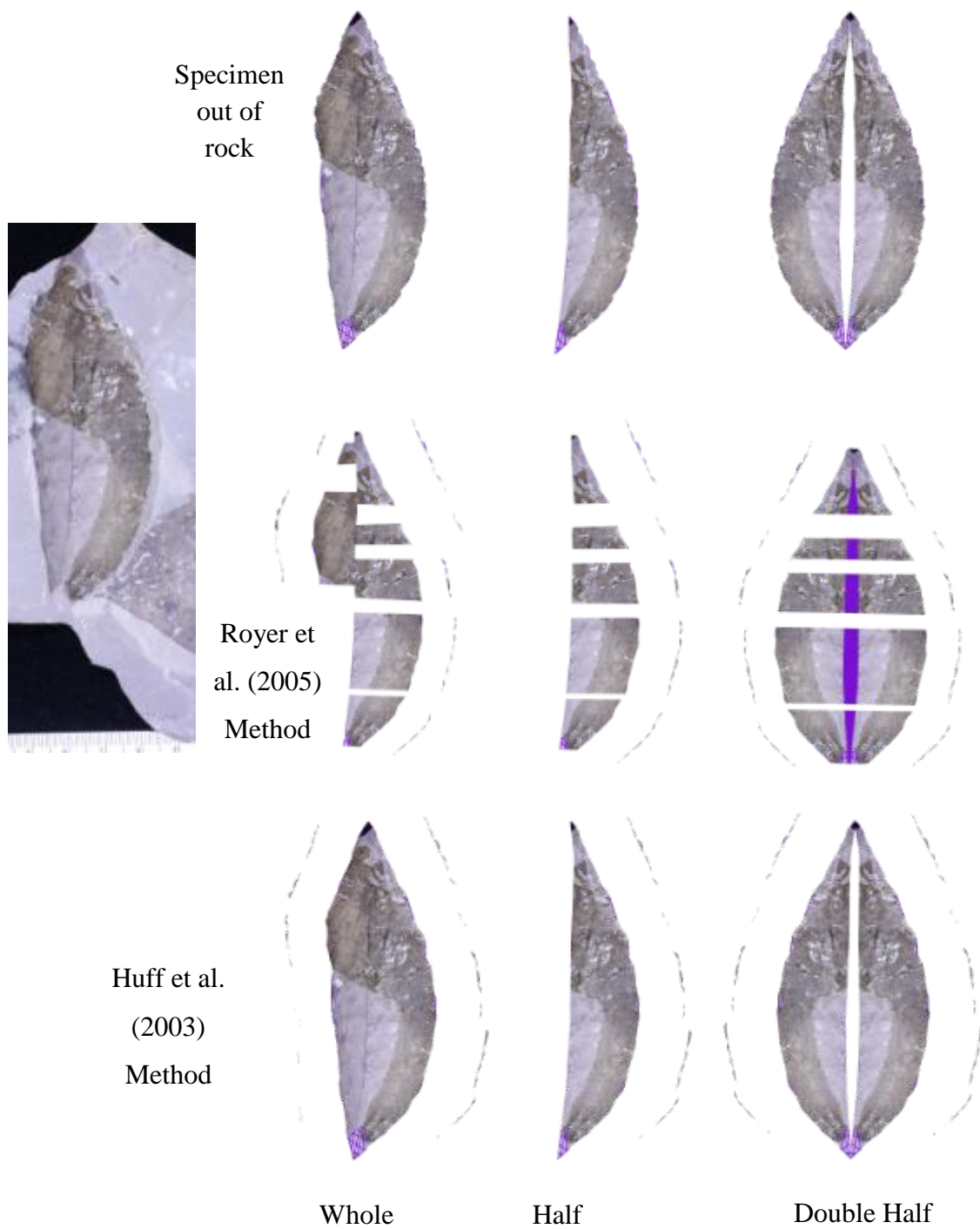
Illustration 6. Dicot 4 16369
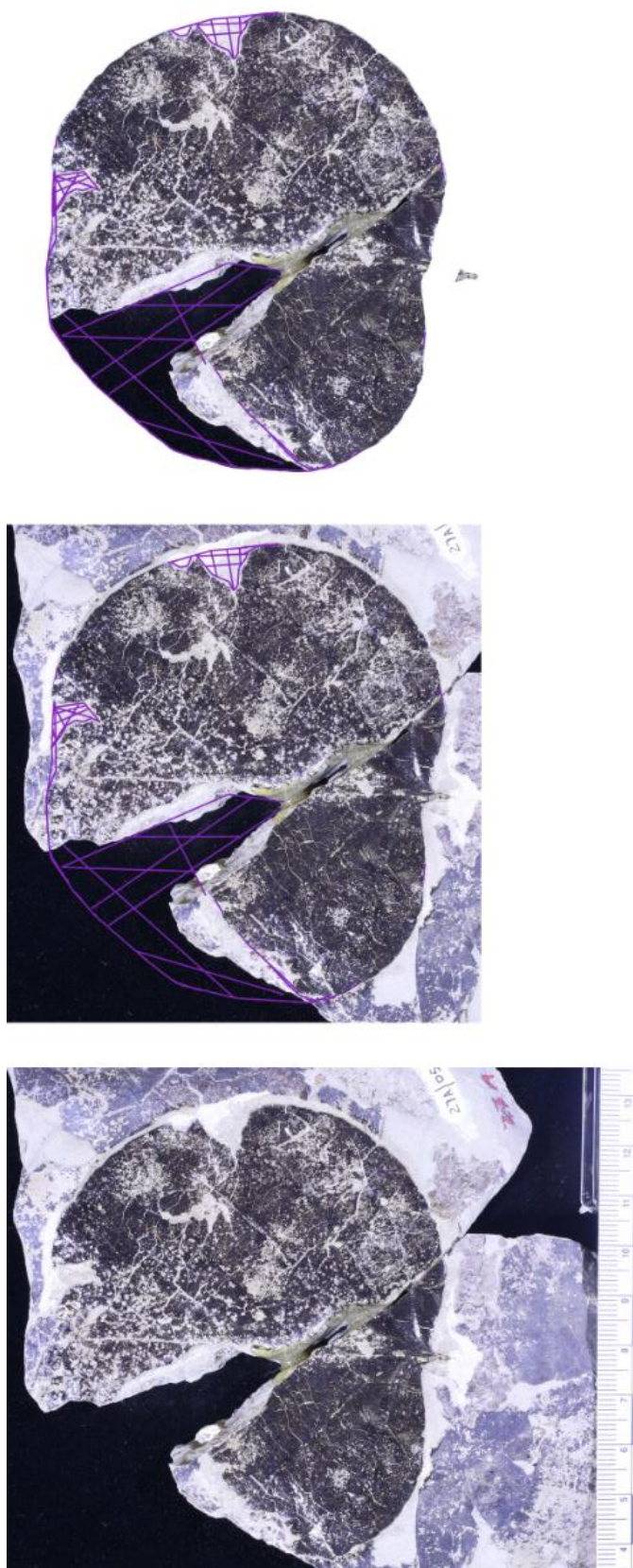
Illustration 7. Dicot 5 16425

96
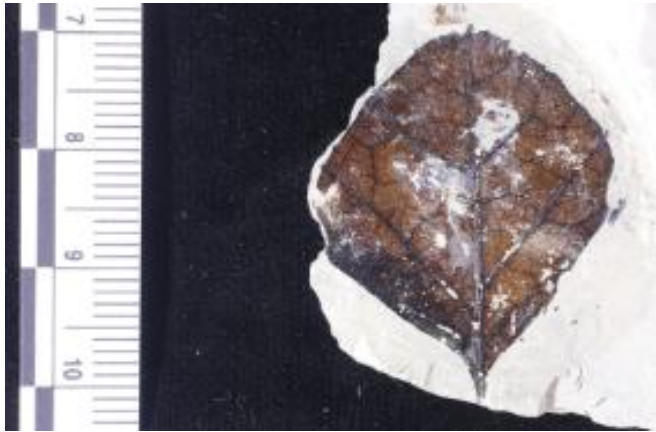
Illustration 8. Dicot 6 16405
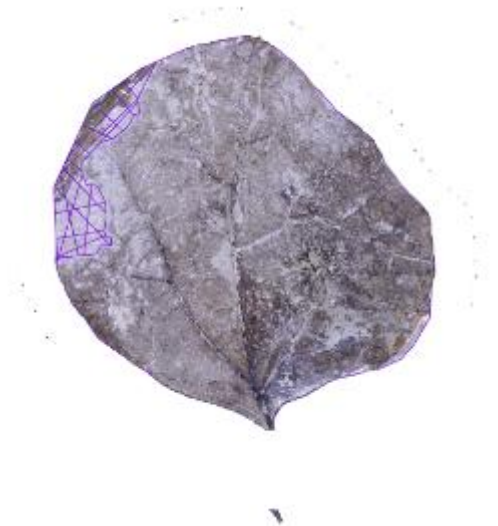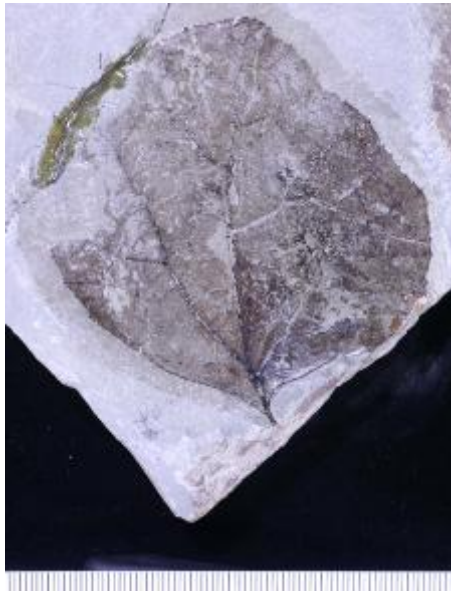
Illustration 9. Dicot 6 16420

Illustration 10. Dicot 7 42A/07/001
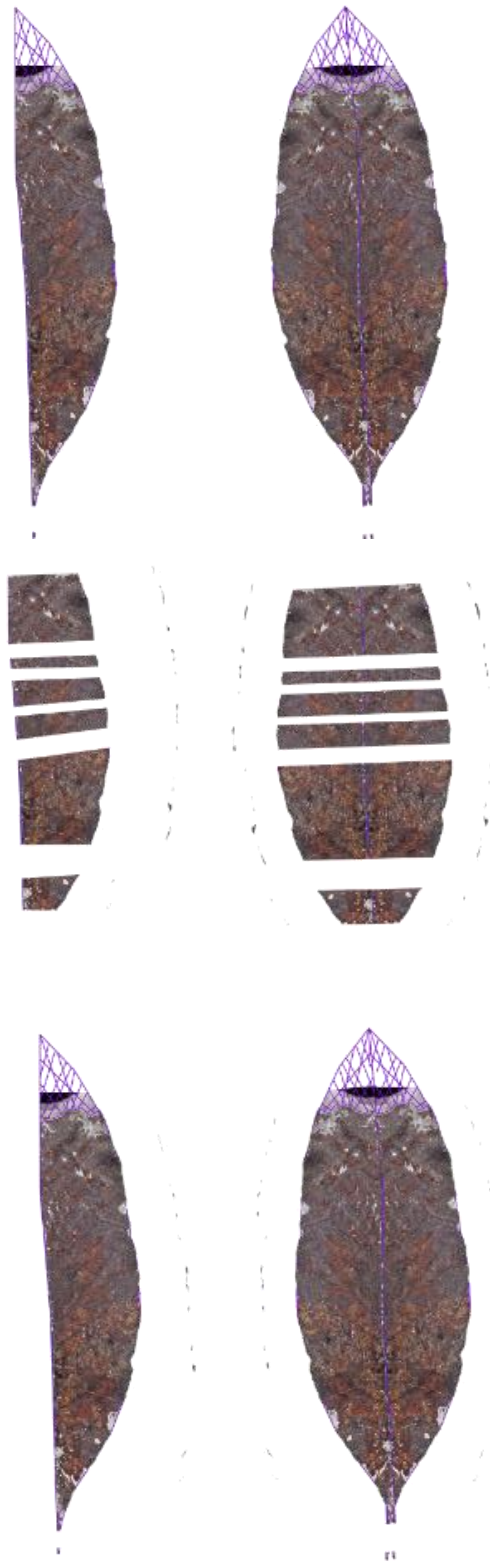
Illustration 11. Dicot 9 loc 1902 (no label)

Illustration 12. Dicot 10 16431

Illustration 13. Dicot 11 16396
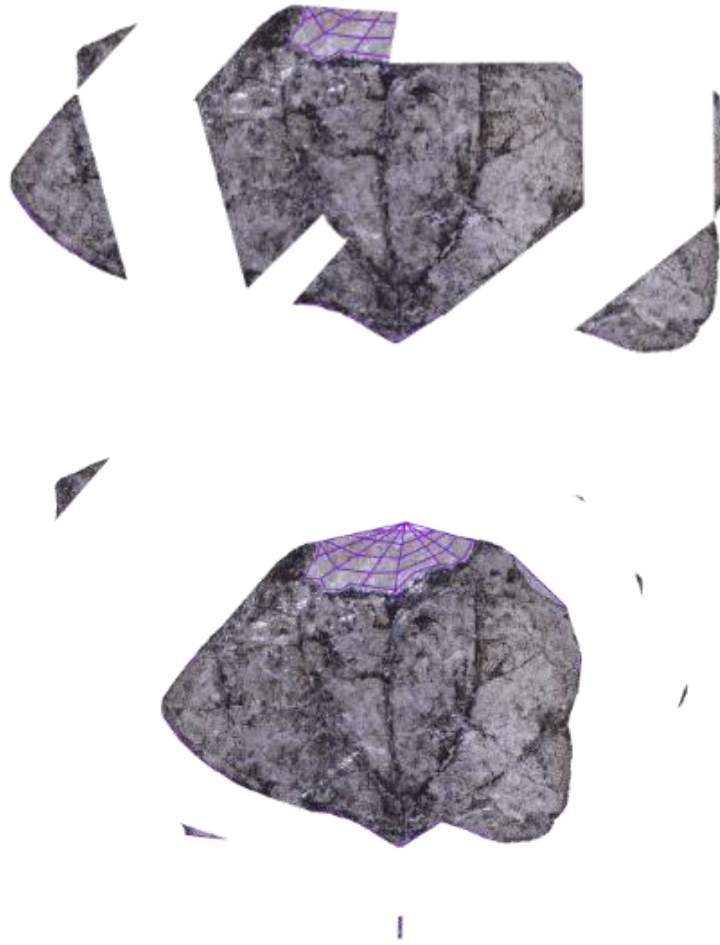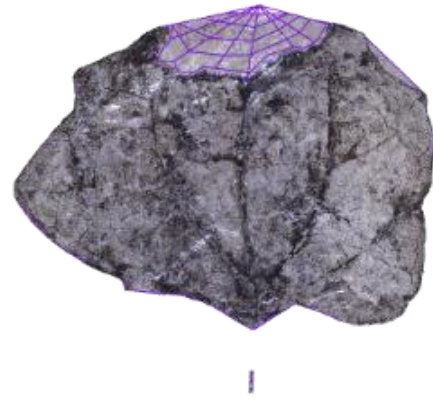
Illustration 14. Dicot 17 16427

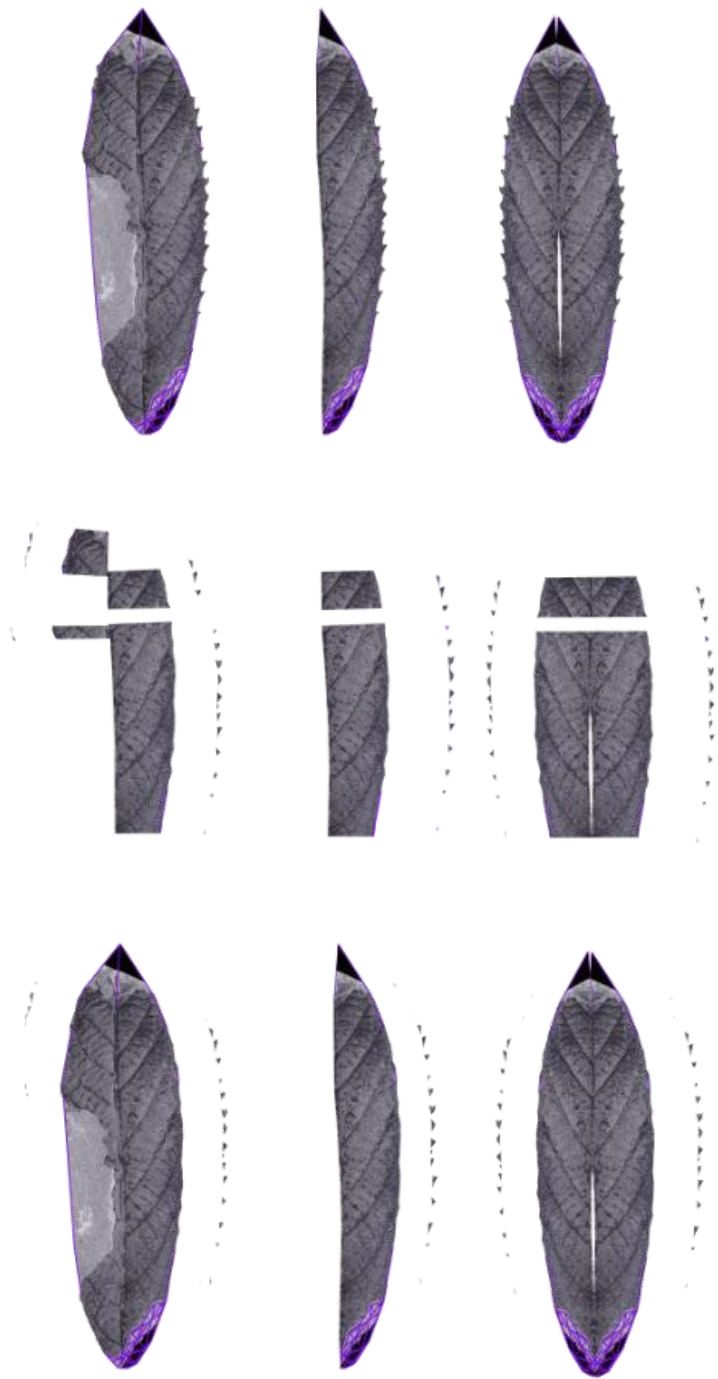**Illustration 15.** Dicot 25 16275

Illustration 16. Dicot 25 16281

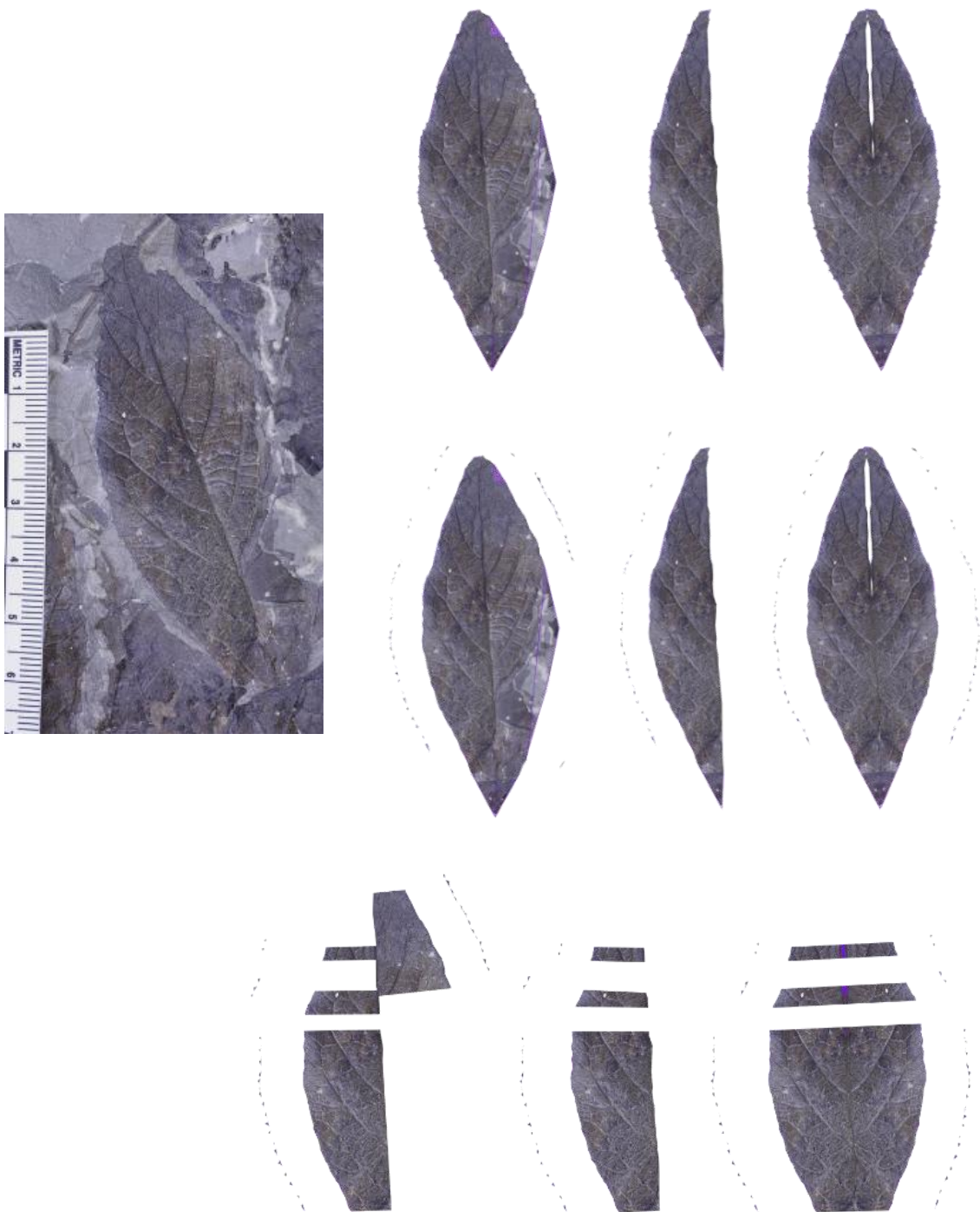**Illustration 17.** Dicot 25 16292

Illustration 18. Dicot 25 16388
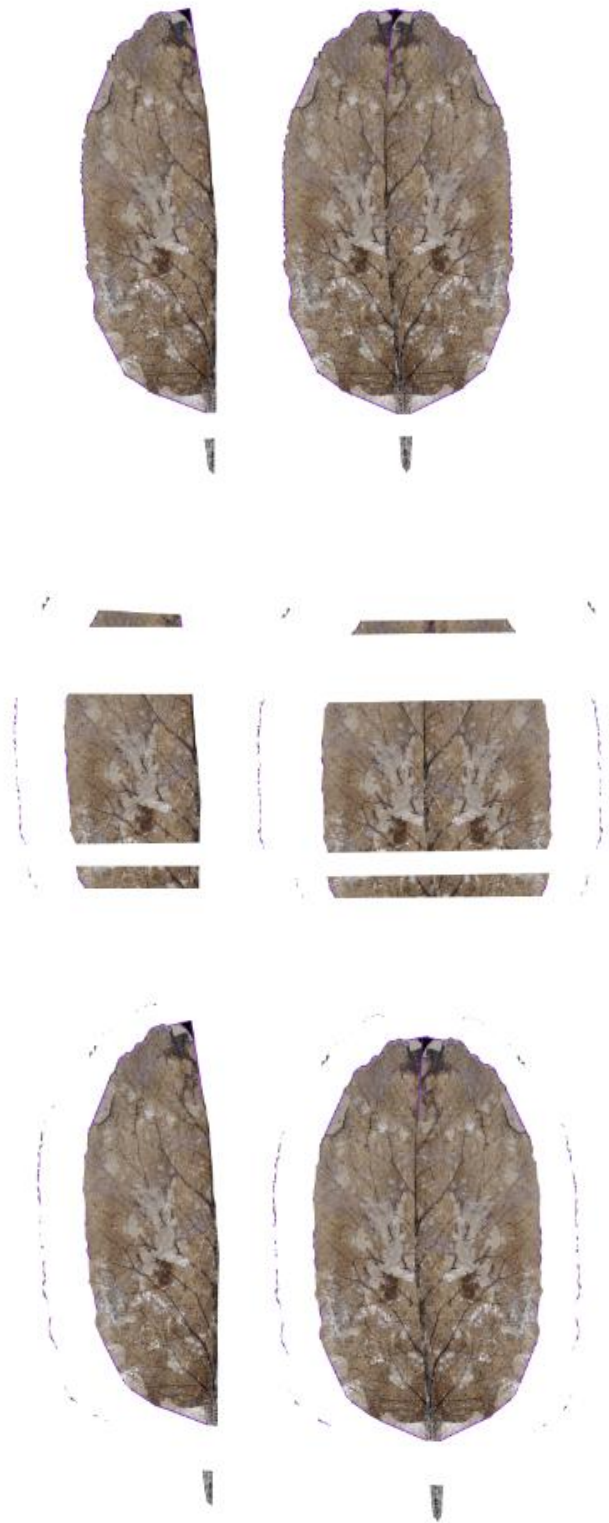
Illustration 19. Dicot 25 16409 (A)

Illustration 20. Dicot 27 16371
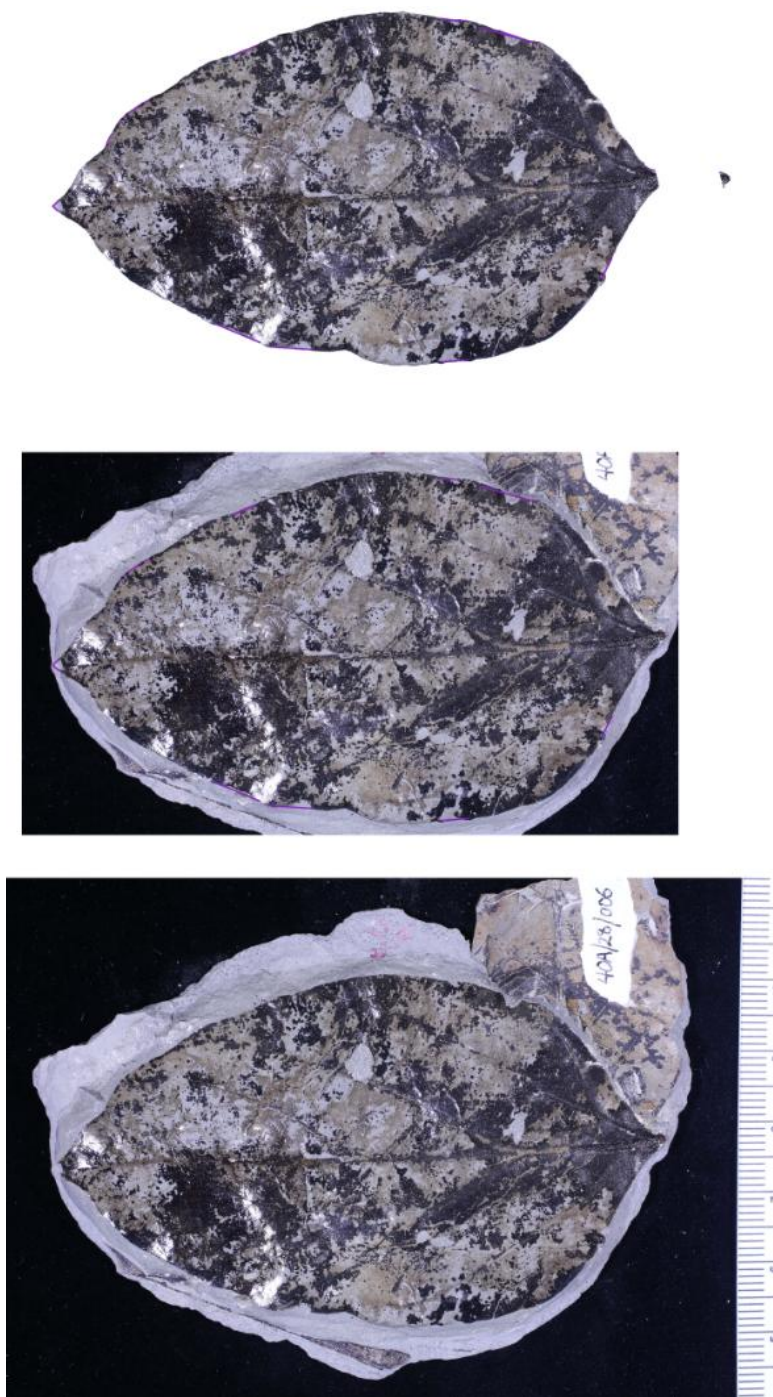
Illustration 21. Dicot 28 116389 (B)
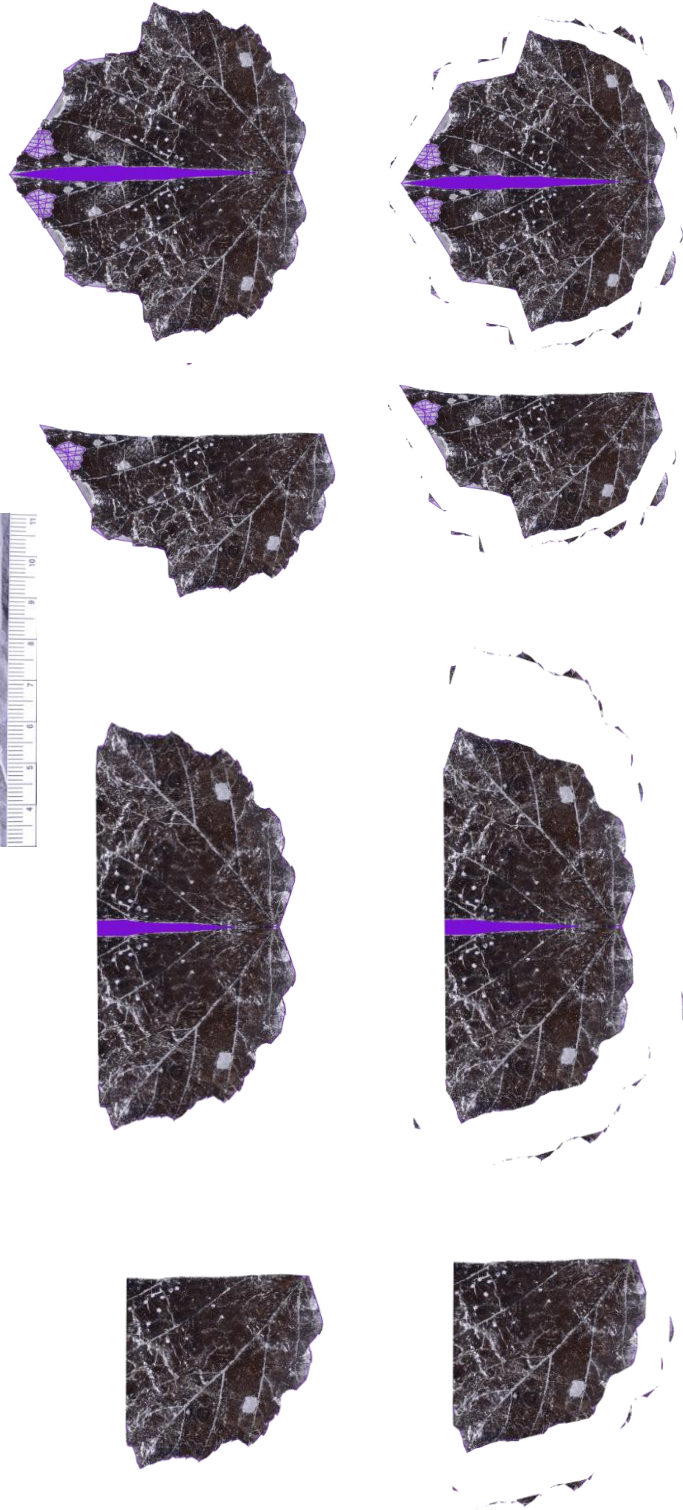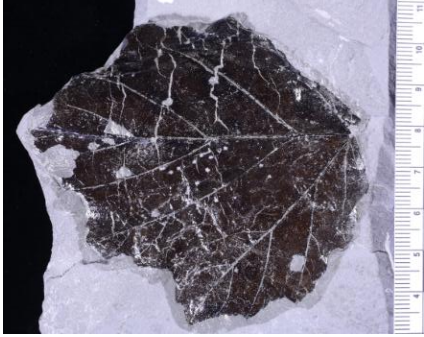
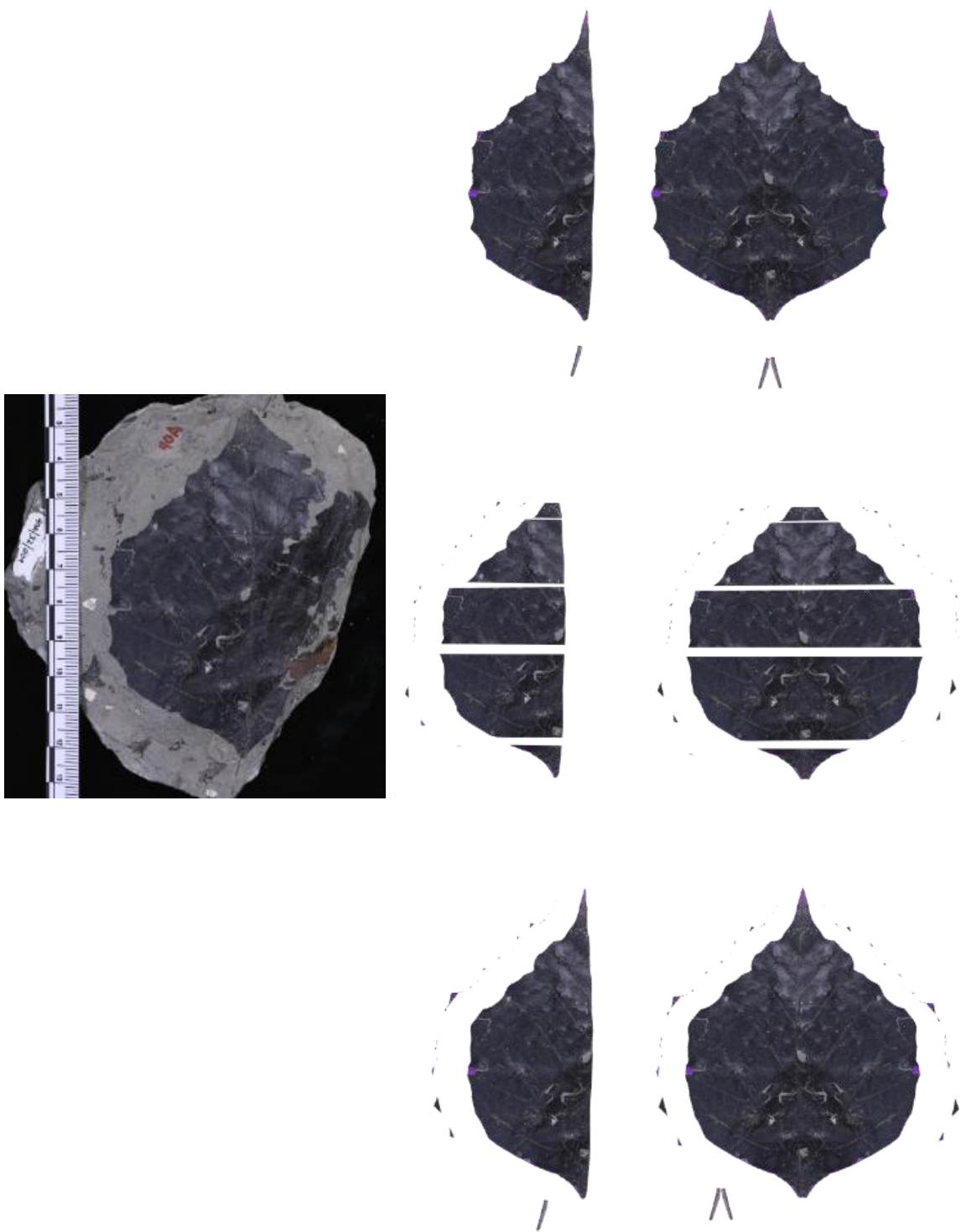**Illustration 22.** Dicot 28 16426

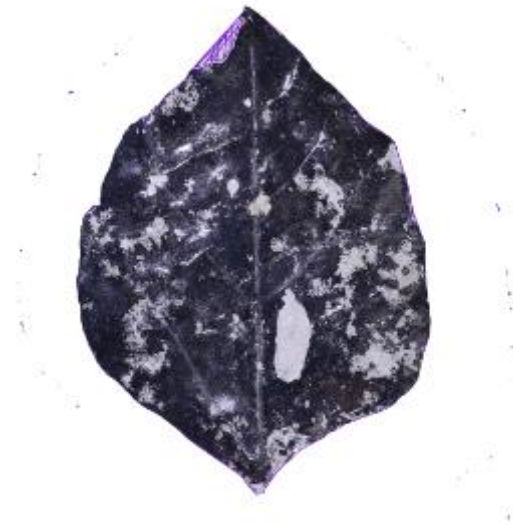**Illustration 23.** Dicot 30 16419

Illustration 24. Dicot 32 16400
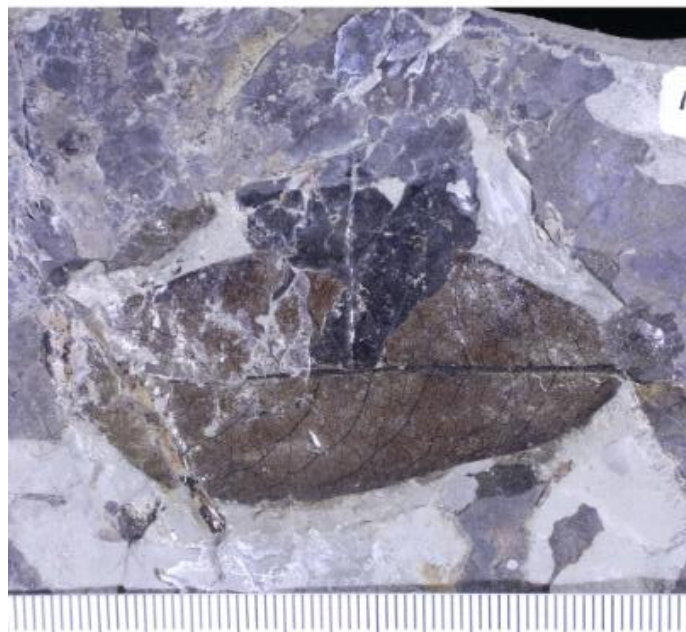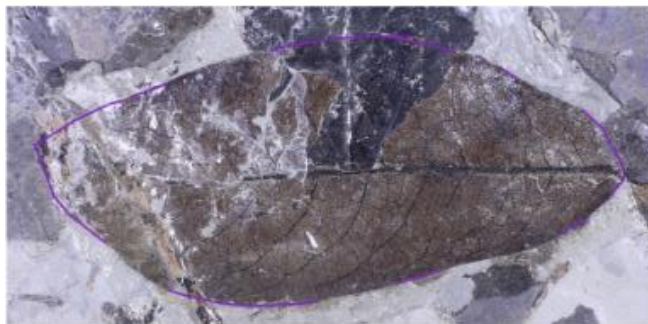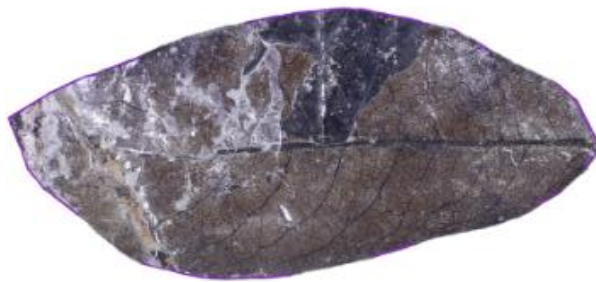
Illustration 25. Dicot 32 16402

Illustration 26. Dicot 43 16411

115

Illustration 27. Dicot Unknown #1 16331

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