USING FOSSIL PLANTS TO UNDERSTAND GLOBAL CHANGE: EVIDENCE FOR PALEOCENE-EOCENE WARMING IN THE GREATER GREEN RIVER BASIN OF SOUTHWESTERN WYOMING

Peter Wilf

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ABSTRACT

USING FOSSIL PLANTS TO UNDERSTAND GLOBAL CHANGE: EVIDENCE FOR PALEOCENE-EOCENE WARMING IN THE GREATER GREEN RIVER BASIN OF SOUTHWESTERN WYOMING

Peter Wilf

Scott L. Wing

The fossil record offers the only opportunity to observe the effects of global change in an extended time series. I analyze two methods for estimating past mean annual temperature and precipitation from assemblages of fossil leaves: leaf-margin and leaf-area analysis, respectively. These and other approaches are applied to diverse and well preserved paleofloras from the Greater Green River Basin of southwestern Wyoming in order to study climatic and biotic change during an interval of pronounced global warming, the late Paleocene (Tiffanian and Clarkforkian) and early Eocene (Wasatchian and earliest Bridgerian). Vegetational response to climate change in the study area was strongly pronounced. The Clarkforkian was humid and subtropical, following cooler humid conditions in the Tiffanian. Many plant families with modern tropical affinities immigrated in the Clarkforkian, but diversity remained as low as in the Tiffanian. Temperatures peaked in the mid-Wasatchian, the time of the Cenozoic thermal maximum, and a turnover of over 80% of species occurred from the Clarkforkian to the Wasatchian that included the immigration of a second wave of plant families with modern tropical affinities. Mid-Wasatchian vegetation was more diverse than that of the Clarkforkian and was derived from humid, subtropical swamp forest. A second major species turnover occurred from the Wasatchian to the earliest Bridgerian, accompanying severe drying and slight cooling. The source vegetation consisted of subtropical scrub growing on the margins of a playa lake system in a more arid and seasonal climate. Predominantly frost-free conditions were present throughout the study interval, with the exception of the Tiffanian and possibly portions of the Graybullian. Although the Eocene Green River lake system has been suggested as a factor contributing to mild southern Wyoming winters, this study shows that equable climates existed during several time intervals when lakes were either not present or not fully developed.

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CHAPTER ONE

INTRODUCTION

The recent recognition of the possibility of anthropogenic global warming has led to accelerated research into the biotic effects of pronounced climate change (e.g., Walker and Steffen, 1996; Watson et al., 1996). As there are no data from the future, most of our information about this potentially warm world is derived from computer simulations at several scales. These range from global climate simulations (Semtner and Chervin, 1992; Thompson and Pollard, 1995) to “patch models” that simulate changes in local vegetational dynamics (e.g., Smith et al., 1996).

The fossil record offers the only means to observe the biotic effects of long-term climate change directly and to test computer models on a differently configured world. Paleontology therefore has a vital part to play as a checkpoint in the debate over modern climate. While paleontological data from marine sections is of the utmost importance, data from continental areas are at least as essential. The world’s population lives on land, and continental data can provide information on a regional scale. While computer models have succeeded in simulating first-order effects, they have, to date, frequently failed to provide accurate “predictions” for any particular region, either in the present world or in the past (e.g., Covey et al., 1996).

The sensitivity of vascular plants to climate is well known. This dissertation addresses the importance of paleobotanical data in understanding past climates. I first explore methods for inferring past climates from fossil plants. These methods and many others are then applied to improve understanding of one of the most dramatic global warming events in Earth history, which occurred in the late Paleocene-early Eocene interval and produced the warmest temperatures of the Cenozoic during the early

Eocene (Zachos et al., 1994). For this purpose, I present results of the first major paleobotanical field study of the Paleocene-Eocene transition in southern Wyoming.

A brief overview of each chapter follows here. Detailed introductions and literature reviews appear within the individual chapters.

Chapter 2, “When are leaves good thermometers? A new case for Leaf Margin Analysis”, argues that a long-recognized method for inferring climates from leaf assemblages is at least as precise as more recent and considerably more labor-intensive approaches. Bailey and Sinnott (1915) first proposed this method, now known as leaf-margin analysis. It is based on the strongly positive correlation in mesic forests between mean annual temperature and the percentage of species in an assemblage with untoothed leaf margins. The chapter includes mathematical analyses, results of field transect studies in Pennsylvania and Puerto Rico, and an extensive leaf-margin data set.

Chapter 3, “Using fossil leaves as paleoprecipitation indicators: An Eocene example”, presents a new method, leaf-area analysis, for estimating mean annual precipitation from leaf assemblages. I document a highly significant positive correlation between the natural logarithm of mean annual precipitation and the mean natural logarithm of the species’ leaf areas in a vegetation sample. The data set supporting the correlation is derived from the literature; the samples are from the West Indies, North, Central, and South America, and West Africa. Leaf-area analysis is applied to seven Eocene floras from the Western United States, using data provided by coauthors S. L. Wing, D. R. Greenwood, and C. L. Greenwood.

The next three chapters present results from my paleobotanical field work in southwestern Wyoming. Chapter 4, “Portrait of a late Paleocene (early Clarkforkian) terrestrial ecosystem: Big Multi Quarry and associated strata, Washakie Basin, southwestern Wyoming", is an interdisciplinary field study of an 18 m section that contains well-preserved fauna and flora in close stratigraphic association. The study area has exceptional biostratigraphic importance because it contains Big Multi Quarry, the most diverse fossil mammal locality from the Clarkforkian Land Mammal Age (approximately the last one million years of the Paleocene). With coauthors K. C. Beard and J. W. Norejko, who provided the faunal analyses, and K. S. Davies-Vollum, who analyzed sediments, I present and implement a total-evidence approach for interpreting paleoclimates and paleoenvironments. The chapter also includes floral and faunal lists.

Chapter 5, "Paleobotanical analysis of late Paleocene-early Eocene climate changes in the Greater Green River Basin of southwestern Wyoming", is an overview of changes in climate, environments, floristic composition, plant community structure, and diversity for the entire late Paleocene and early Eocene. This chapter also includes a revised stratigraphic scheme, a preliminary systematic list of the flora, and a complete listing of plant fossil localities.

Chapter 6, "The flora", presents preliminary descriptive information for the fossil flora. Included are a complete matrix of species by localities and 38 plates illustrating reference specimens.

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CHAPTER TWO

WHEN ARE LEAVES GOOD THERMOMETERS? A NEW CASE FOR LEAF MARGIN ANALYSIS

This chapter is written in the style of the journal *Paleobiology*, where it has been published (v. 23, p. 373-390, 1997). I have also included three data appendices that could not be included in the journal article because of space considerations (Appendices 2.4-2.6).

When are leaves good thermometers? A new case for Leaf Margin Analysis

Peter Wilf

Abstract.—Precise estimates of past temperatures are critical for understanding the evolution of organisms and the physical biosphere, and data from continental areas are an indispensable complement to the marine record of stable isotopes. Climate is considered to be a primary selective force on leaf morphology, and two widely used methods exist for estimating past mean annual temperatures from assemblages of fossil leaves. The first approach, Leaf Margin Analysis, is univariate, based on the positive correlation in modern forests between mean annual temperature and the proportion of species in a flora with untoothed leaf margins. The second approach, known as the Climate-Leaf Analysis Multivariate Program, is based on a modern data set that is multivariate. I argue here that the simpler, univariate approach will give paleotemperature estimates at least as precise as the multivariate method because (1) the temperature signal in the multivariate data set is dominated by the leaf-margin character; (2) the additional characters add minimal statistical precision, and in practical use do not appear to improve the quality of the estimate; (3) the predictor samples in the univariate data set contain at least twice as many species as those in the multivariate data set; and (4) the presence of numerous sites in the multivariate data set that are both dry and extremely cold depresses temperature estimates for moist and nonfrigid paleofloras by about 2°C, unless the dry and cold sites are excluded from the predictor set.

New data from Western Hemisphere forests are used to test the univariate and multivariate methods and to compare observed vs. predicted error distributions for temperature estimates as a function of species richness. Leaf Margin Analysis provides excellent estimates of mean annual temperature for nine floral samples. Estimated temperatures given by 16 floral subsamples are very close both to actual temperatures and to the estimates from the samples. Temperature estimates based on the multivariate data set for four of the subsamples were generally less accurate than the estimates from Leaf Margin Analysis. Leaf-margin data from 45 transect collections demonstrate that sampling of low-diversity floras at extremely local scales can result in biased leaf-margin percentages because species abundance patterns are uneven. For climate analysis, both modern and fossil floras should be sampled over an area sufficient to minimize this bias and to maximize recovered species richness within a given climate.

Peter Wilf. Department of Geology, Hayden Hall, University of Pennsylvania,
Philadelphia, Pennsylvania 19104
Present address: *Department of Paleobiology, MRC 121, National Museum of Natural*
History, Smithsonian Institution, Washington, D.C. 20560. E-mail: wilfp@nmnh.si.edu

Introduction

Understanding global change requires knowledge of terrestrial as well as marine climates, both past and present. The marine record offers detailed paleotemperature data for approximately the past 100 million years, primarily from stable isotope ratios (e.g., Savin 1977; Zachos et al. 1994). On land, the morphologic characteristics of fossil plant assemblages, in particular the leaves of flowering plants, are considered to be useful sources of proxy data for past climates. The fossil record of flowering plants is temporally comparable to the marine isotope record, dating to the Early Cretaceous (e.g., Taylor and Hickey 1996), although leaf-climate relationships have undoubtedly changed through time. The primary role of leaves as photosynthetic organs requires that their morphologies be climatically tuned for photosynthetic efficiency. Many correlations of the sizes and shapes of modern leaves to climatic conditions are statistically significant and have been used in a uniformitarian manner to quantify past climates (e.g., Wolfe 1993). How best to apply this uniformitarian procedure is still controversial.

Bailey and Sinnott (1915, 1916) observed a robust positive relationship between climatic warmth and the percentage of dicotyledonous species in a flora that have leaves with entire margins (i.e., untoothed, smooth edges), suggesting that this relationship be used as a paleothermometer that is independent of taxonomy. After a number of initial paleoclimatic studies (Berry 1916; Chaney and Sanborn 1933; Wolfe and Hopkins 1967; Wolfe 1971, 1978), Wolfe (1979) published a linear regression of mean annual temperature (MAT) vs. the percentage of woody dicot species with entire margins in floral samples from eastern Asian forests. These samples are all from forests without significant moisture limitations, and only one sample has MAT << 10°C.

Application of this regression to fossil floras to estimate past MAT is known as Leaf Margin Analysis (LMA).

Paleotemperature estimates from Leaf Margin Analysis have shown general agreement with other geologic proxies, such as marine temperature trends (Wolfe and Poore 1982; Parrish and Spicer 1988; Johnson and Hickey 1990; Stott and Kennett 1990; Huber and Watkins 1992; Johnson and Wilf 1996); diversity patterns for reptiles (Hutchison 1982); and stable oxygen isotope ratios of hematite encrustations on bones of fossil mammals (Koch et al. 1996).

The physiological basis of the MAT vs. leaf-margin correlation has never been adequately demonstrated. However, teeth are strongly associated with the movement of water out of leaves via transpiration and guttation (Haberlandt 1914; Bailey and Sinnott 1916; Canny 1990; Wilson et al. 1991; Wolfe 1993), which suggests that one of the functions of teeth in colder climates is to boost sap flow. Leaf teeth typically have large veins running directly to their apices and often contain conspicuous open pores, or hydathodes (e.g., Haberlandt 1914; Bailey and Sinnott 1916; Canny 1990). As spikes projecting from the leaf margin with veins running to the end of the ‘spike,’ teeth thin the boundary layer and create transpiration hot spots (Canny 1990). Tracer dyes rapidly move toward teeth (Canny 1990), and Wolfe has observed that leaf-clearing chemicals are forcibly ejected from many tooth apices (Wolfe 1993: p. 61). Toothed species are also uncommon in dry, saline, frigid or otherwise moisture-limiting environments (e.g., Bailey and Sinnott 1915, 1916). Givnish (1979) proposed that untoothed margins correlate to leaf thickness, and in turn to temperature, because the decreased flow resistance in thicker leaves allows more even growth between secondary veins, resulting in a smoother margin. Roth et al. (1995), in a hydrodynamic modeling study, suggested that some teeth are byproducts of differential expansion near large veins that run to the margin. This growth strategy may be cost-effective for the frequent leaf regeneration required of deciduous plants (Mosbrugger and Roth 1996).

Wolfe (1993) attempted to improve the precision of paleotemperature estimates and to provide a method for inference of other climatic variables, including seasonality of temperature and amount and seasonality of rainfall, with the Climate-Leaf Analysis Multivariate Program (CLAMP). This approach uses a multivariate data set, primarily from North American forests, of 29 leaf characters per sampling site, including leaf-margin type. Unlike the LMA data set, CLAMP contains a large number of samples from dry and severely cold areas. The CLAMP data set and accompanying meteorological data are ordinated onto two axes using correspondence analysis (Hill 1974). Quantitative climate estimates for a fossil flora are derived by scoring each species in the flora for all of the 29 CLAMP characters, ordinating the resulting vector along with the CLAMP data set to obtain the two axis scores for the fossil sample, and following a graphical procedure to correlate these scores to polynomial fits of the data set for each climate variable (see Wolfe 1993). A revised version of CLAMP that uses canonical correspondence analysis has been developed (Wolfe 1995), but the modified data set is not yet published.

The climatic significance of the majority of the CLAMP characters, other than leaf-margin type, remains largely speculative. The best-substantiated theories link moisture to leaf size (e.g., Webb 1968; Givnish 1979) and to the presence of drip-tips, which are attenuate, elongate leaf apices that appear to control the rate of water clearance (e.g., Dean and Smith 1978; Richards 1996). The relatively long and narrow drip-tip enables water flowing as a sheet to form droplets that are large enough to break the surface tension over this narrow area (H. Pfefferkorn personal communication 1997).

A series of studies have utilized the CLAMP ordination approach to estimate past MAT and other climatic variables (Wolfe 1990, 1992, 1994a,b,c; Povey et al. 1994; Herman and Spicer 1996, 1997). The CLAMP data set has also been analyzed through multiple regression, which results in the elimination of the majority of the characters as statistically insignificant (Gregory and Chase 1992; Wing and Greenwood 1993; Gregory 1994; Greenwood and Wing 1995; Gregory and McIntosh 1996; but see Wolfe 1995: Fig. 2). A few tests of CLAMP-based multiple regressions in modern forests have, for the most part, resulted in poor estimates for temperature variables besides MAT and in overestimates of precipitation (Jacobs and Deino 1996; Wilf 1996, unpublished data; Burnham in press). Recently, Jordan (1996; see Wing and Greenwood 1996) has shown that the temperature signal in the CLAMP data set is statistically dominated by MAT and that CLAMP-derived estimates of cold-month mean temperature (CMM) are byproducts of the modern correlation between MAT and CMM. The utility of the CLAMP data set for estimating variables besides mean annual temperature is therefore poorly substantiated.

Are leaves better thermometers when multivariate techniques based on the CLAMP data set are used, or is Leaf Margin Analysis, the simpler approach, at least as precise? I argue here for the latter. From both a theoretical and a practical standpoint, I examine whether including characters in addition to leaf-margin type improves MAT estimates. I analyze sources of noise in the CLAMP and LMA data sets that are related to the numbers of species scored per sample, sampling scale, the types of samples used, and the scoring process. I then use these analyses to predict how MAT estimates derived from the CLAMP data set should differ from LMA estimates and how MAT estimates using any method are expected to vary as a function of the number of species scored. The predictions are then tested on new data from living forests.

Materials and Methods: Living Forests

Nine Western Hemisphere floral samples were used in this study, seven tropical and two temperate, containing a total of 1445 species. This figure is a maximum because some of the 62 taxa determined to be distinct species within samples, but not assigned to formal species names, may have been present in more than one sample (e.g., "*Trichilia* sp."). The median sample had 132 species. The nine floras were chosen because they are well studied, allowing the analysis of high numbers of species and the examination of leaf-climate data at more than one spatial scale. Also, the samples represent, albeit unevenly, a wide latitudinal range of about 55°, including two samples from South America, which has been little studied with regard to leaf-climate relationships (Halloy and Mark 1996). Desert sites and frigid sites with little rainfall during the growing season were avoided because the MAT vs. leaf-margin correlation is sensitive to dryness and extreme cold (Bailey and Sinnott 1915, 1916; Dilcher 1973; Wolfe 1979; 1993; Wing and Greenwood 1993; this paper). No preference was given to riparian vs. nonriparian habitats, or to whether or not vine data were available.

Sixteen floral subsamples were taken from the nine samples; the median subsample had 49 species. These subsamples were either field collections or species lists from previously published research plots. Basic data on the samples and subsamples are shown (Table 2.1), and short descriptions are given below.

All available species of native woody dicots were scored for leaf-margin type, whether trees, shrubs, or woody vines (Table 2.1), except for parasites, epiphytes, mangroves (because they typically grow in saline environments), cacti, cactus-like euphorbs, and many succulents. Three woody non-dicots (one *Gnetum*, two *Smilax*) that contribute dicot-like leaves to the forest litter were included.

Following Wolfe (1993), a species received a score of 0 if all of its leaves were toothed, a score of 0.5 if some leaves were toothed, and a score of 1 if all leaves were entire. A tooth was considered to be a vascularized extension of the leaf margin, with a corresponding sinus incised not more than one quarter the distance from margin to midrib. Spines were not counted as teeth, after Wolfe (1993), because they are unvascularized extensions of the leaf whose function may be defensive (Givnish 1979) and not related to climate. Unvascularized crenulations or irregular edges were likewise not scored as teeth. Lobed leaves without teeth on the lobes were scored as entire. Except for the field-collected subsamples scored directly from specimens (Barro Colorado Island, Guánica Forest, York County, Allegheny National Forest), leaves were scored from manuals and from herbarium material at the National Herbarium (US) or the Herbarium of the Botany Department of the Academy of Natural Sciences (PH). Species with ambiguous or conflicting margin descriptions or poor figures in manuals were always herbarium-checked.

The four field-collected subsamples listed above were also scored (Table 2.2) for the CLAMP characters that were used as predictors in the following four regression models for estimating mean annual temperature (Gregory and McIntosh 1996): (1) all sites in the CLAMP data set used as predictors, along with multiple characters; (2) all sites, but only the percentage of entire-margined species used as a predictor variable; (3) only relatively warm sites (CMM < -2°C [see Wing and Greenwood 1993]) used as predictors, multiple characters; and (4) only the warm sites, with just entire-margin percentage as a predictor variable. To avoid any circularity, regression coefficients were adjusted with the Barro Colorado Island (BCI) and Guánica Forest CLAMP sites removed from the predictor set. The former is the same as the BCI subsample in this paper, and the latter was collected near the site of the Guánica Forest subsample. The adjusted models (not shown) were nearly identical to the published models. Except for this adjustment specifically for the purpose of regression analysis of the subsamples, all calculations from the CLAMP data set in this article use the published version (Wolfe 1993).

All species lists generated for this contribution are available by request. Latitude-longitude coordinates are given at the precision available.

Beni Biosphere Reserve, Bolivia.—Leaves were scored from photocopied mini-herbaria and plot lists in Dallmeier et al. (1991a,b) for Beni Biosphere Reserve Biodiversity Plots 1-4, along and near the Curiraba River, near San Borja, Bolivia (14°30'S, 66°18'W). The four plots combined comprised the sample, the individual plots the subsamples. Climate data are given by Dallmeier et al. (1991a), who report a six-month dry season. The plots lie in tropical moist forest (Plots 1-3) and tropical savanna (Plot 4).

Manu Biosphere Reserve, Perú.—Leaves were scored from photocopied mini-herbaria and plot lists in Dallmeier et al. (1993a,b) for Manu Biosphere Reserve Biodiversity Plots 1-4, along and near the Manu River, adjacent to Pakitza Station, Perú (11°55'48"S, 71°15'18"W). The four plots combined comprised the sample, the individual plots the subsamples. Climate data from the Cocha Cashu Biological Station, upriver from Pakitza at 11°54'S,71°22'W (Terborgh 1990), were supplied by J. Terborgh and M. Jarrell. The area is in tropical moist forest, with about five drier months.

Barro Colorado Island, Panamá.—All woody species listed and described in Croat (1978) comprised the sample. The subsample was a collection of BCI leaves made by R. Burnham and S. Wing in 1989 at 9°10’N, 79°51’W from a single hectare of the 50-ha permanent forest plot of Hubbell and Foster (1983). These were the same leaves used as the BCI sample in the CLAMP data set (Wolfe 1993), and they are housed in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution. My rescoring of these leaves was a test of the repeatability of the scores; the new scores were used for the regression analyses. Climate for BCI is reported in Windsor (1990); the forest type is tropical moist forest. The dry season lasts approximately four and a half months.

Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico.—Woody dicot species were those listed in Chinea et al. (1993). The subsample was Bisley Biodiversity Plot 13 (18°18’N, 65°50’ W), scored from the photocopied mini-herbarium in Dallmeier, Kabel et al. (1991c). Precipitation data are as reported in Scatena (1989); the area lies within montane subtropical wet forest, with little rainfall seasonality (Lugo 1986). Temperature data were derived by linear altitudinal interpolation from Brown et al. (1983).

Guánica Commonwealth Forest, Puerto Rico.—Woody species in the sample are those listed in Little and Wadsworth (1964) and Little et al. (1974) as present in Guánica Commonwealth Forest (Lugo et al. 1997). These manuals primarily list tree species but also include many shrubs. Limited transects collected in May, 1995, within a 0.5-km radius of the forest office, at 17°58’27”N, 66°52’09” W, comprised the subsample. A full physiognomic range of each species encountered was included. Voucher specimens are housed in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution. Climate data are from Ensenada, 17°58’N, 66°56’W (Murphy and Lugo 1990). Guánica Forest is a subtropical dry forest. There are two significant dry periods per year, totaling seven to eight months; high temperature and low precipitation make Guánica Forest the driest of the nine samples. One of Wolfe’s (1993) CLAMP sites was also from this area. The Ensenada data used here indicate MAT almost 2°C lower than reported in Wolfe (1993).

St. John, United States Virgin Islands.—Two vegetational zones were scored: dry evergreen woodland and moist forest (Woodbury and Weaver 1987; Acevedo-Rodríguez 1996). Species lists for the zones given in Woodbury and Weaver (1987) were revised following Acevedo-Rodríguez (1996). Three research plots comprised the subsamples. St. John Biodiversity Plot 1 (Dallmeier, Comiskey, and Ray 1993c) on Caneel Hill, Virgin Islands National Park (18°21’N, 64°44’W), lies within the dry evergreen formation. The two moist forest sites were Bordeaux Mountain and L’Esperance in the central part of the island (Reilly et al. 1990). Climate data are from Cruz Bay, near Caneel Hill, for dry woodland, and from Lameshur Bay, south of Bordeaux Mountain, for moist forest (Woodbury and Weaver 1987). The dry season throughout St. John is about four months.

Pennsylvania: York County and Allegheny National Forest.—Species lists of trees, shrubs, and woody vines for the York County and Allegheny National Forest (ANF) floral samples were generated by A. Rhoads from the computerized version of the Pennsylvania Flora Database (Rhoads and Klein 1993). For ANF, the query was a latitude-longitude grid containing all of western McKean County, northwestern Pennsylvania, which includes the National Forest. The species list for York County, southeastern Pennsylvania, was generated by the county name. The query areas were large in order to capture adequate numbers of species for analysis from these low-diversity floras.

Although temperature varies within these regions, effects on the analysis were minimized by selecting climate stations as close as possible to the latitudinal and altitudinal centers of the sampled areas. For York County and ANF respectively, these were York SSW3 Pumping Station, at 39°55'N, 76°45'W, 118 m elevation, and Bradford 4 SW Reservoir 5, 41°53'31"N, 78°42'52"W, 503 m. Climate data were supplied by P. Knight. The York County area has even precipitation throughout the year, while for ANF there is a slight drop in precipitation in January and February; ANF is the coldest sample, with a January mean temperature of -5.8°C. The York County and Allegheny National Forest study areas respectively belong to the Appalachian oak forest and Allegheny hardwood forest types.

The York County and Allegheny National Forest subsamples were each collected in October, 1995, at the respective times of maximum abscission, within a range of less than 250 m of altitude and less than 15' of latitude. Both subsamples were composed of multiple transects for leaf collection, with 28 transects for ANF and 17 in the eastern portion of York County. Ten of the ANF transects and seven of the York County transects were collected along rivers and streams, the rest on slopes and ridge crests. Each transect consisted of three parallel linear subtransects, 40 m in length and spaced 10 m apart. Individual parautochthonous assemblages of fossil leaves from single quarry sites are thought to represent a similar source area of vegetation, so these transects were spatially analogous to such sites (Burnham et al. 1992; Wing and DiMichele 1995). For each transect, I collected the full physiognomic range found for the leaves of all species encountered on the transect lines. Leaves were collected both from litter, to include the physiognomy of canopy leaves, and directly from live twigs, to maximize the number of species and facilitate identification. *Betula alleghaniensis* Britton (toothed) and *Cephalanthus occidentalis* L. (entire) were encountered but not included in the subsample list. Leaves of the former had dried and disintegrated prior to abscission, and no leaves of the latter could be found. Voucher specimens and field maps are housed in the Botany Department of the Morris Arboretum, University of Pennsylvania. All species-locality data have been submitted for inclusion in the Pennsylvania Flora Database.

The Importance of Leaf-margin Type

Analysis.—The proportion of entire-margined species is the CLAMP character that explains, by far, the most variance in estimated MAT. This character offers important additional advantages in that its relationship to temperature is well documented, and it is easily and unambiguously scored for nearly all modern leaves and for all but the most poorly preserved fossils. There is also no taphonomic bias in this character that has been rigorously substantiated (Roth and Dilcher 1978; Greenwood 1992; Burnham 1994).

The CLAMP ordination itself provides the clearest evidence of the dominance of leaf-margin type in the temperature signal from leaves. The MAT and no-teeth vectors are so coincident that Wolfe projected directly to the no-teeth vector in his bivariate plots used to estimate MAT (Wolfe 1993: Fig. 11, Plate 4).

The dominance of margin type is also clear in multiple regression analyses of the CLAMP data set. The Gregory and McIntosh (1996) multiple regression for MAT based on the 74 CLAMP sites with cold-month mean temperature greater than -2°C has a standard error of 1.5°C ($r^2 = 0.92$, $F = 170$, $p < 0.0005$). Rerunning this multiple regression as specified and examining the standardized coefficients for the predictor variables shows that the proportion of entire-margined leaves controls 67% of the MAT signal (standardized coefficient of 0.67). The univariate MAT vs. leaf-margin regression in the same table, using the same subset of 74 sites, has only 0.6°C more standard error, 2.1°C ($r^2 = 0.84$, $F = 390$, $p < 0.0005$).

Can Additional Variables Increase Precision?—While the extra 0.6°C of resolution predicted by multivariate analysis is possible in theory, it may not yet be attainable in practice. Small errors in any of the scores used in multivariate models (Table 2.2), whether caused by scoring methodology or taphonomy, can easily affect the value of the temperature estimate by more than 0.6°C; for example, a 7% error in the score for leptophyll 2 is sufficient in the model based on the 74 warm CLAMP sites of Gregory and McIntosh (1996). Accurate scoring of the size distributions of leaves in fossil floras is especially problematic because large leaves are preferentially removed during transportation, and a precise correction method has not been found (Roth and Dilcher 1978; Greenwood 1992). Also, the CLAMP scoring procedures specified in Wolfe (1993) have never been tested for consistency among investigators and may not be reproducible at the precision needed, even for modern samples. The rescoring of the BCI subsample for this paper differed substantially from the published scores in Wolfe (1993) for both acute bases and emarginate apices (Table 2.2), but not for the proportion of entire-margined species. In an informal experiment, I asked eight paleontologists, five of them paleobotanists, to score, independently, voucher specimens of the same six randomly chosen species from the Barro Colorado Island subsample for presence or absence of an acute base. The instructions were to follow exactly the definition given in Wolfe (1993: p. 28): “a base is acute if the most basal fourth of the lamina has a straight or concave margin.” There was 100% agreement for two species, 75% agreement for three species, and 63% agreement for one species. The participants reported that the complexity of basal curvatures exhibited by the specimens was greater than the definition could accommodate, leading to uncertainty in scoring, for example, if there were both concave and convex portions of the margin of the basal fourth.

Expected Differences between CLAMP and LMA Estimates.— The dominance of leaf-margin type predicts that differences among estimated MATs from different data sets primarily depend on the fits of MAT vs. leaf-margin percentage in those data sets. Linear regressions are shown (Fig. 2.1) for the following: Leaf Margin Analysis (Wolfe 1979); the full CLAMP data set of Wolfe (1993); the warm CLAMP subset, containing only sites with CMM greater than -2°C; and the samples scored for this paper. The presence of numerous dry and cold sites in the CLAMP data set but not in the LMA data set explains much of the difference between the CLAMP and LMA regressions. Dry and cold sites have the same margin percentages as warmer, moister sites. For example, the 32 CLAMP sites with CMM less than -2°C, most of which receive very little moisture during the growing season, have an average of 25.4% entire-margined species, which gives an averaged estimated MAT from Leaf Margin Analysis of 8.9°C. The actual average MAT for these sites, however, is only 4.5°C. The effect of the cold outliers is to pull down the regression line from the CLAMP data set on the left side; when removed (gray line in Fig. 2.1), the vertical-intercept becomes higher and the slope lower than for all of the other fits shown, and standard error decreases significantly.

The regression lines for the warm subset and for LMA cross at 34% entire margins (Fig. 2.1). Multivariate MAT estimates that use all sites in the CLAMP data set as predictors, and estimates derived from the warm subset for floras with more than about 34% entire-margined species should be, on average, cooler than MAT estimates from the same leaves estimated with LMA. Floras with less than about 34% entire margins will generally give higher multivariate MAT estimates than Leaf Margin Analysis if the warm subset is used.

Quantification of Sampling Error

Analysis.—Leaf-margin type is essentially a binomial character. Only a small percentage of species bear both toothed and entire leaves, creating a third outcome (3.7% of the species scored for this study). Assuming random sampling of leaf margins, binomial probability predicts that the standard deviation of an observed leaf-margin percentage is a function of the number of species scored, just as the standard deviation of the outcome of a weighted coin-toss experiment is a function of the number of trials.

Suppose that r species are selected at random from an unlimited species pool, and a proportion P, $0 < P < 1$, of the r species have entire margins. After repeating this experiment many times, the standard deviation of P, $\sigma[P]$, will be

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

which is the equation for the standard deviation of binomially distributed outcomes (see also Raup 1991). The equation for Leaf Margin Analysis, based on the Wolfe (1979) data set, is (Wing and Greenwood 1993)

$$\mathrm{LMAT} = 30.6P + 1.14 \tag{2}$$

where LMAT is the *leaf-estimated mean annual temperature*. Constants have no variance, so if c and d are constants, then

$$\sigma[cP + d] = c\sigma[P]\ . \tag{3}$$

Combining equations (1), (2), and (3), the standard deviation of LMAT, in degrees C, is

$$\sigma[\mathrm{LMAT}] = c\sqrt{\frac{P\,(1-P)}{r}} \tag{4}$$

where c is the slope of the MAT vs. leaf-margin regression in the data set used. In this paper, $c = 30.6$, from equation (2), will be applied. The standard deviation that is the output of equation (4) will be referred to as the "sampling error" or the "binomial sampling error" (Fig. 2.2). Equation (4) also applies to multivariate estimates of MAT because margin type is the dominant character in predicting MAT, even in multivariate models. For 50% entire margins, binomial sampling error is near 3°C at 26 species and near 2°C at 59 species. The 80% or 20% entire-margins case is more generous, with 17 species required for 3°C of sampling error and 37 for 2°C. For most fossil floras, sampling error exceeds the standard errors of published methods for estimating paleotemperature (Wing and Greenwood 1993; Wolfe 1993; Gregory and McIntosh 1996).

Suppose that a subsample of r species is taken from a particular floral sample. If the sample contains m entire and n toothed species, and P is now the observed proportion of entire margins in the subsample, the standard deviation of P is

$$\sigma_{m+n}[P] = \sigma(\mathrm{m, n, r}) = \frac{1}{m+n}\sqrt{\frac{mn(m+n-r)}{r(m+n-1)}} \quad . \qquad 5)$$

For the derivation and demonstration of the convergence of equation (5) to equation (1) as $m + n \rightarrow \infty$, see Appendix 2.1. The standard deviation of LMAT of the subsample from the LMAT of the sample is then

$$\sigma_{m+n}[\mathrm{LMAT}] = \frac{c}{m+n}\sqrt{\frac{mn(m+n-r)}{r(m+n-1)}} \quad . \qquad 6)$$

The standard deviation function of equation (6) is shown (Fig. 2.3) for $m = n$ (50% entire margins) and samples of $m + n$ = 100, 250, and ∞ species. The latter value gives the same curve as equation (4), with $P = 0.5$. As the number of species in the subsample approaches the number in the sample, ever fewer combinations of species are possible, and the standard deviation goes to zero.

Application of the Sampling Error Model to MAT Estimation.—The equation for binomial sampling error (eq. 4) makes the conservative, worst-case assumption that the flora that is being sampled has infinite species richness. There are two major reasons why this is a practical assumption. First, it is difficult, even in the most fortunate situations, to make better than an order-of-magnitude estimate of the true diversity of the regional flora from which any fossil assemblage was drawn (e.g., Anderson et al. 1996). By assuming an infinite flora, this issue is moot. Second, the difference between the standard deviations for the "infinite" vs. "finite" cases is negligible (Fig. 2.3), except for the unusual case of depauperate floras that have been exceptionally well sampled.

The appropriate error placed on a particular estimate of past MAT is the larger of the two error figures given by binomial sampling error and the standard error on the regression used. For the latter, unfortunately, it is not yet clear what value to apply. The LMA regression of Wolfe (1979) has a standard error of ± 0.8°C (Wing and Greenwood 1993). This extremely low value is unlikely to be reproduced in other data sets. For example, an individual sample, using 25% entire margins, would have to contain 274 species just for its binomial sampling error to be this low. Standard error for an LMA-type regression using the full CLAMP data set is ± 3.4°C; with the coldest sites removed it is ± 2.1°C (Fig. 2.1). Standard error for MAT vs. leaf-margin regression using the nine floral samples scored for this study is ± 2.0°C. Until additional speciose data sets are published from mesic forests without extreme winter temperatures, the distribution of standard error values will be unknown. On the basis of the regression from nine samples, I suggest a provisional minimum error for paleotemperature estimates of ± 2°C, to be used when binomial sampling error is less than 2°C.

Range of Temperature in Data Sets.—Construction of leaf-margin data sets that are statistically robust requires a range of temperature among samples such that there is an adequate ratio of temperature range to database noise. In county-scale studies in the

Carolinas (Dolph and Dilcher 1979) and Indiana (Dolph 1984), no strong correlation between leaf-margin type and temperature was found. However, both areas have limited temperature ranges that are close to the 4°C (± 2°C) suggested minimum noise level (Carolinas: about 6°C; Indiana: about 3°C).

Relative Noise among Data Sets.—The equation for binomial sampling error (eq. 4) can be used to approximate the relative amount of statistical noise in the LMA and CLAMP data sets. Most of the samples that comprise the LMA data set contain more than 50 species (Wolfe 1993: p. 4), whereas the CLAMP data set has a median of 28 species per sample (Fig. 2.4). If 50% of the flora has entire margins, then sampling error is less than 2.2°C for more than 50 species, but for 28 species, it is 2.9°C (Fig. 2.2), a noise gap of more than 0.7°C. For this reason, combining leaf-margin data from CLAMP and LMA into a single database is not recommended.

Results and Discussion: Living Forests

Leaf Margin Analysis: Floral Samples.—Results are shown in Table 2.3. The samples were sufficient to generate a statistically robust MAT vs. leaf-margin relationship (Fig. 2.1). This nine-sample regression is much closer to the fit for Leaf Margin Analysis than to the fits of the CLAMP data set (Fig. 2.1), although all four regression lines are broadly similar.

Leaf Margin Analysis: Floral Subsamples.—The subsamples performed well as thermometers in comparison to the samples (Table 2.4). Four of the subsamples gave better temperature estimates (negative error difference in Table 2.4), and five subsamples gave LMAT that was the same or only 0.1°C worse than the samples (error difference = 0 or 0.1). Excluding Beni 4, a subsample of only nine species, the subsamples correlated nearly as well as the samples in MAT vs. leaf-margin regression ($r^2 = 0.84$, SE = ± 2.4°C, $F = 71$, $p < 0.0005$).

To examine whether LMAT changes in a predictable fashion with sample size, equation (6) was applied to each subsample to generate a standard deviation, which was compared to the observed deviation of subsample LMAT from sample LMAT (Table 2.4, Fig. 2.5). Observed deviations, in absolute value, are less than standard deviations for 14 of the 16 subsamples, or 88%, more than the expected value of 68% associated with one standard deviation. The subsample LMATs are therefore more like the sample LMATs than expected from random sampling of margin type.

Leaf Margin Analysis vs. CLAMP-based Regression.—When both LMA and the CLAMP data set were used to estimate MAT from four subsamples (Table 2.5), Leaf Margin Analysis results had less total error than any of the four CLAMP-based models. The maximum LMA error was 2.5°C, while each CLAMP-derived regression model generated at least one error figure greater than 3°C. The multivariate CLAMP-based estimates were not more accurate in absolute sum than their univariate counterparts, despite their lower standard errors (Gregory and McIntosh 1996), and multivariate maximum errors were greater. The sum of errors row in Table 2.5 shows a distinct negative bias in the CLAMP-based scores, principally from the severe underestimates for Barro Colorado Island.

The differences between the estimates for “univariate all,” “univariate warm,” and LMA (Table 2.5) are the result of the different regression lines used (Fig. 2.1). “Multivariate warm” results, in identical fashion to the “univariate warm” estimates, are cooler than LMA for the tropical sites and warmer than LMA for the temperate sites. The "multivariate all" estimates, like "univariate all", are lower than the LMA estimates, except for York County and ANF. Six of the eight multivariate estimates therefore are higher or lower than the LMA estimates as predicted by the leaf-margin character alone, a reasonable percentage given that the latter controls about 70% of the temperature signal.

The poor multivariate results for BCI probably reflect the lack of moist tropical sites in the CLAMP data set. For example, the character for emarginate (notched) apices is highly correlated with MAT in CLAMP and is included in the regression models used here. A leaf cannot have both an emarginate apex and a drip-tip at the same time. Therefore, in tropical forests with high drip-tip percentages, like BCI, the percentage of species with emarginate apices is likely to be lower than in drier climates with the same MAT. If few wet tropical forests are in the predictor set, MAT will probably be underestimated for warm floras with a high percentage of drip-tips.

Effects of Nonrandom Species Abundance Patterns: Pennsylvania Transects.— Plant species in natural communities generally do not occur with equal abundance. The probability of sampling a margin type will rarely equal the proportion of species in the source flora having that margin type. The leaf-margin percentage of the species present in a local area will differ both from the regional flora and from nearby sampling locations (Gentry 1969; Dolph 1971, 1979; Burnham 1994). The smaller the collection area and the fewer species present, the more significant the possible leaf-margin bias.

These points are demonstrated by the transect data from York County and Allegheny National Forest (Fig. 2.6, Appendix 2.2). The differences in LMAT for individual transects and whole samples are not evenly distributed; neither distribution in Figure 2.6 has a mean or mode near zero. While inconsistent LMAT from such species-poor collections is expected, each set of transects has a bias that reflects the species abundance patterns of the two floras. All but one of the 17 York County transects is more entire than the York sample as a whole, resulting in higher LMAT (mean difference = 3.3°C, σ of differences = 1.9°C). In contrast, all but five of the 28 ANF transects are more toothed than the ANF sample, giving lower LMAT (mean difference = -4.4°C, σ of differences = 3.6°C). The modal percentage of entire-margined species for the ANF transects is 0.

The frequencies of occurrence of individual species further illustrate the nonrandom patterns of species distribution in these Pennsylvania floras (Appendix 2.3). In the York County sample, many entire-margined species are ubiquitous in transects, but this margin type makes up a minority of the total woody species (28.0%; Table 2.3). In the ANF area, the toothed species are both ubiquitous and a majority of the species (24.3% entire; Table 2.3). The ubiquity of entire-margined species in the York transects causes the right-shift of the distribution of estimate differences in Fig. 2.6, while for ANF, the ubiquity of toothed species results in a left-shift.

These Pennsylvania transects are spatially, if not depositionally, analogous to the source areas of single quarry sites containing fossil leaves deposited in low-transport environments (Burnham et al. 1992; Wing and DiMichele 1995), illustrating that leaf-margin percentages of fossil samples that are highly localized and also have low species richness can be affected by uneven species abundance patterns as well as by sampling error. The latter can always be quantified using the methods in this paper, even in a fossil assemblage. However, the possibility of nonrandom sampling of margin types from the source flora (Fig. 2.6) is much more difficult to evaluate in fossil floras and is best countered at a particular stratigraphic level by maximizing recovered diversity, number of replicate samples, transect length, and number of facies types sampled (Burnham 1989).

Similarly, modern predictor samples should be collected over an area large enough to account for site-to-site physiognomic variation in the vegetation being sampled and to be spatially analogous to multiple rather than single quarry sites of fossils. Special care must be taken when sampling is spatially restricted, for example, to a close radius around a climate station. In such a case, the investigator should demonstrate, by examining the vegetation in surrounding areas, that the gain in microclimatic resolution is greater than the loss to sampling error and local bias in margin type. The “finite flora” method (eq. 5) can be used to evaluate the latter by comparing observed deviations vs. standard deviations of the leaf-margin percentages of vegetational subsamples in relation to a corresponding sample. Also, the distribution of the leaf-margin percentages of subsamples relative to that of the sample can be examined for unidirectional biases (Fig. 2.6).

This study also points out a hazard of inferring climate from the proportion of *leaves* possessing physiognomic characters, rather than the proportion of *species* (Greenwood 1992). The former is highly influenced by abundance patterns that may have no climatic significance.

Conclusions

Estimates of mean annual temperature based on Leaf Margin Analysis are at least as precise as those derived from the CLAMP data set. Leaf-margin type dominates the temperature signal in dicot leaf physiognomy and, in mesic and nonfrigid climates, the proportion of species in a flora that have untoothed margins is an excellent thermometer. Use of the additional characters from CLAMP contributes little information about temperature. These characters probably can not be scored reliably enough to make use of this additional information, either in modern or fossil floras.

The number of species per sample has a major effect on the precision of MAT estimates, both in predictor data sets and in fossil samples for which an MAT estimate is desired. This sampling error can be quantified, if sampling is random with respect to margin type, using a simple equation based on the standard deviation of binomially distributed outcomes. The minimum error placed on an MAT estimate using either LMA or the CLAMP data set should be about $\pm 2^{\circ}$C, or the binomial sampling error when the latter is greater.

In practice, the assumption of random sampling of margin types from a regional flora will usually be violated because species abundance patterns are uneven. The effects of nonrandom sampling in fossil floras are best overcome by maximizing the number of species, the number of facies, and the transect length sampled per stratigraphic level. Predictor data sets should be collected over a sufficient area to minimize local biases caused by species abundance patterns and to maximize the number of species scored within a given climate.

Leaf Margin Analysis remains the most effective, unambiguous, and simply applied method for estimating past land temperatures, providing an invaluable complement to the marine stable isotope record. In the future this method and new multivariate approaches may be improved considerably by (1) constructing new predictor data sets that contain highly speciose samples and cover a wide temperature range, especially in the Southern Hemisphere, and (2) physiological studies to determine the biological bases of the correlations of leaf physiognomy to climatic variables.

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TABLE 2.1. Collection and meteorological data for the nine floral samples and 16 subsamples; subsample data in italics: (1) mean annual temperature, °C, (MAT); (2) mean annual precipitation, cm (MAP); (3) number of species scored; (4) area covered by samples or collection type of subsamples; and (5) vegetation sampled. See text for citations.

Sample or *subsample*	MAT	MAP	#Species	Collection area or *type*	Species scored
Beni Biodiversity Plots, Bolivia	27	180	104	4 ha	trees ≥ 10 cm dbh
Plot 1			*43*	*1 ha plot*	*trees ≥ 10 cm dbh*
Plot 2			*49*	*1 ha plot*	*trees ≥ 10 cm dbh*
Plot 3			*44*	*1 ha plot*	*trees ≥ 10 cm dbh*
Plot 4			*9*	*1 ha plot*	*trees ≥ 10 cm dbh*
Manu Biodiversity Plots, Perú	24.2	243	292	4.4 ha	trees ≥ 10 cm dbh
Plot 1			*127*	*1 ha plot*	*trees ≥ 10 cm dbh*
Plot 2			*159*	*1.4 ha plot*	*trees ≥ 10 cm dbh*
Plot 3			*101*	*1 ha plot*	*trees ≥ 10 cm dbh*
Plot 4			*64*	*1 ha plot*	*trees ≥ 10 cm dbh*
Barro Colorado Island, Panamá	27.1	261	629	1560 ha	all woody species
Burnham and Wing collection			*137*	*1 ha plot*	*trees ≥ 1 cm dbh*
Bisley Watersheds, Puerto Rico	24.4	350	131	≈ 20 ha	all woody species
Biodiversity Plot			*31*	*1 ha plot*	*trees ≥ 10 cm dbh*
Guánica Commonwealth Forest, Puerto Rico	25.1	86	126	4016 ha	trees and shrubs
subsample			*26*	*limited local transects*	*trees and shrubs*
St. John, U.S. Virgin Islands, dry woodland	26.9	113	173	1730 ha	all woody species
Biodiversity Plot			*48*	*1 ha plot*	*trees ≥ 4 cm dbh*
St. John, U.S. Virgin Islands, moist forest	26.3	120	227	860 ha	all woody species
L'Esperance			*35*	*0.5 ha plot*	*all stems ≥ 5 cm dbh*
Bordeaux			*57*	*1 ha plot*	*all stems ≥ 5 cm dbh*
York County, Pennsylvania	11.8	104	132	2.35 X 10^5 ha	all woody species
subsample			*56*	*17 local transects*	*all woody species*
Allegheny National Forest area, Pennsylvania	7.2	116	74	≈1.27 X 10^5 ha	all woody species
subsample			*47*	*28 local transects*	*all woody species*

TABLE 2.2. Physiognomic scores for multiple regression analysis, Barro Colorado Island (BCI), Guánica Forest, York County, and Allegheny National Forest subsamples, shown as proportions. The two rows for BCI show, respectively, the scores from Wolfe (1993: Table 2) and the rescoring of the same leaves for this paper. Scores for the proportions of entire-margined species (Table 2.4) were the same for both scorings of BCI. Characters scored following instructions in Wolfe (1993): (1) lobed leaf, (2) leptophyll 2 (size category), (3) emarginate apex (i.e. notched apex), (4) acute base, and (5, 6) two categories of length:width ratios, < 1 and 1-2.

Subsample	Lobed	Lepto 2	Apex em.	Base acute	L:w < 1	L:w 1-2
BCI (Wolfe 1993)	0.02	0.01	0.12	0.66	0.03	0.18
BCI (this paper)	0.026	0.012	0.036	0.161	0.029	*
Guánica Forest	0	0.109	0.538	0.404	0.013	0.525
York County	0.232	0.018	0.054	0.277	0.098	0.491
Allegheny National Forest	0.202	0.011	0.043	0.106	0.096	0.386

* Not scored separately for BCI; 0.18 was used for regression.

TABLE 2.3. Leaf-margin data for the nine floral samples: (1) proportion of entire-margined species; (2) leaf-estimated mean annual temperature (LMAT), in °C; (3) error of the estimate, LMAT - actual MAT; and (4) binomial sampling error, in °C (eq. 4).

Sample	Entire	LMAT	Error of estimate	Sampling error
Beni Biodiversity Plots	0.832	26.6	-0.4	1.1
Manu Biodiversity Plots	0.872	27.8	3.6	0.6
Barro Colorado Island	0.797	25.5	-1.6	0.5
Bisley Watersheds	0.783	25.1	0.7	1.1
Guánica Forest	0.864	27.6	2.5	0.9
St. John, dry woodland	0.795	25.5	-1.4	0.9
St. John, moist forest	0.822	26.3	0.0	0.8
York County	0.280	9.7	-2.1	1.2
Allegheny National Forest	0.243	8.6	1.4	1.5

TABLE 2.4. Leaf-margin data for the 16 floral subsamples and comparisons to corresponding data from full samples: (1) proportion of entire-margined species; (2) leaf-estimated mean annual temperature (LMAT) (eq. 2), °C; (3) error of the estimate, LMAT - MAT; (4) sampling error, °C (eq. 4) ; (5) error difference between each subsample and its sample, calculated as │LMAT (subsample) - MAT│ - │LMAT (sample) - MAT│, some apparent discrepancies due to rounding; (6) observed deviation of the estimate, LMAT (subsample) - LMAT (sample); (7) the expected estimate difference of one standard deviation between subsamples and samples, °C (eq. 6); and (8) the percentage of the species in the sample represented by the subsample.

Subsample	Entire	LMAT	Error of estimate	Sampling error	Error difference	Observed deviation	Standard deviation	%Species
Beni Biodiversity Plot 1	0.860	27.5	0.5	1.6	0.1	0.9	1.3	41.3
Beni Biodiversity Plot 2	0.857	27.4	0.4	1.5	0.0	0.8	1.2	47.1
Beni Biodiversity Plot 3	0.807	25.8	-1.2	1.8	0.8	-0.8	1.3	42.3
Beni Biodiversity Plot 4	0.667	21.5	-5.5	4.8	5.1	-5.1	3.7	8.7
Manu Biodiversity Plot 1	0.862	27.5	3.3	0.9	-0.3	-0.3	0.7	43.5
Manu Biodiversity Plot 2	0.868	27.7	3.5	0.8	-0.1	-0.1	0.5	54.5
Manu Biodiversity Plot 3	0.871	27.8	3.6	1.0	0.0	0.0	0.8	34.6
Manu Biodiversity Plot 4	0.891	28.4	4.2	1.2	0.6	0.6	1.1	21.9
Barro Colorado Island	0.807	25.8	-1.3	1.0	-0.3	0.3	0.9	21.8
Bisley Biodiversity Plot	0.823	26.3	1.9	2.1	1.2	1.2	2.0	22.8
Guánica Forest	0.846	27.0	1.9	2.2	-0.5	-0.5	1.8	20.6
St. John Biodiversity Plot	0.927	29.5	2.6	1.1	1.2	4.0	1.5	27.7
St. John, L'Esperance	0.829	26.5	0.2	1.9	0.2	0.2	1.8	15.4
St. John, Bordeaux	0.816	26.1	-0.2	1.6	0.2	-0.2	1.3	25.1

TABLE 2.4

Subsample	Entire	LMAT	Error of estimate	Sampling error	Error difference	Observed deviation	Standard deviation	%Species
York County	0.277	9.6	-2.2	1.8	0.1	-0.1	1.4	42.4
Allegheny National Forest	0.245	8.6	1.4	1.9	0.0	0.0	1.2	63.5

TABLE 2.5. Errors of regression estimates (estimate - actual) from four subsamples for mean annual temperature, in °C, using both Leaf Margin Analysis and the CLAMP data set. Predictor data used for estimates, from left to right: (1) Leaf Margin Analysis data set; (2) all CLAMP sites, multiple predictor variables; (3) all CLAMP sites, one predictor; (4) the "warm" CLAMP sites with CMM > -2°C, multiple predictors; and (5) "warm" sites, one predictor. Column totals shown both as sums and as sums of absolute values.

Subsample	LMAT - MAT	(MAT estimated from CLAMP data set) - MAT			
		Multivariate, all	Univariate, all	Multivariate, warm	Univariate, warm
BCI	-1.6	-7.7	-4.2	-6.1	-4.4
Guánica Forest	2.5	-0.6	-0.8	-0.3	-1.3
York County	-2.1	0.7	-3.8	0.0	-1.6
Allegheny National Forest	1.4	1.8	-0.2	3.1	2.2
Sum of errors	0.1	-5.8	-9.0	-3.3	-5.1
Sum of absolute errors	7.6	10.8	9.0	9.5	9.5

FIGURE 2.1. Fits of mean annual temperature vs. the proportion of entire-margined species, with plots of the nine floral samples scored in this paper. The solid line is the regression using the nine samples: MAT = 28.6P + 2.24 (r^2 = 0.94, SE = ±2.0°C, F = 102, $p < 0.0005$), where P is the observed proportion of entire-margined species. The dashed line is from the Wolfe (1979) East Asian data set: MAT = 30.6P + 1.14 (r^2 = 0.98, SE = ±0.8°C, F not available, $p < 0.001$). The dotted line is from the CLAMP data set (Wolfe 1993): MAT = 29.1P - 0.266 (r^2 = 0.76, SE = ±3.4°C, F = 333, $p < 0.0005$), and the gray line is from the CLAMP data set when the 32 sites with the coldest winter temperatures are removed prior to regression: MAT = 24.4P + 3.25 (r^2 = 0.84, SE = ±2.1°C, F = 384, $p < 0.0005$). Error bars are one standard deviation (eq. 1).

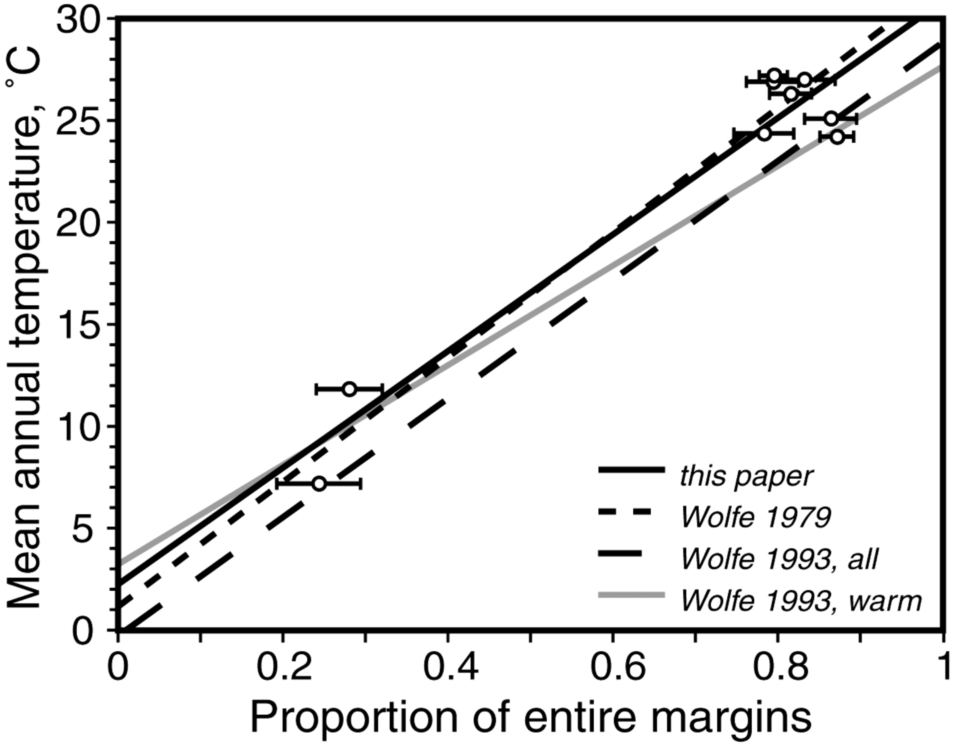
FIGURE 2.2. Sampling error for Leaf Margin Analysis as a function of the number of species scored. Plotted from equation (4), using P = 0.5 (50% entire-margined species) and P = 0.8 (80% or 20% entire).

FIGURE 2.3. The standard deviations of temperatures estimated from Leaf Margin Analysis of subsamples when the means are temperatures estimated from Leaf Margin Analysis of samples. Combined plots from equation (6), using 50% entire-margins and samples of 100, 250 and ∞ species.

FIGURE 2.4. Distribution of the number of species per sample for the 106 samples in the CLAMP database (Wolfe 1993). The single outlier is the collection from Barro Colorado Island, Panamá.

FIGURE 2.5. Observed deviations vs. standard deviations of leaf-estimated mean annual temperature (LMAT) for the 16 floral subsamples in relation to the samples containing them. Data from Table 2.4, in absolute value. Labeled outliers: Beni Biodiversity Plot 4 (Beni4) and St. John Biodiversity Plot (SJBP).

FIGURE 2.6. Estimated mean annual temperatures, using Leaf Margin Analysis, derived from each of 45 Pennsylvania transects (Appendix 2.2) minus the estimated temperatures given by the corresponding York County and Allegheny National Forest samples (York, ANF) (Table 2.3), shown as proportional distributions. Individual transects in these floras tend to have leaf-margin percentages that are greater (York) or less (ANF) than the leaf-margin percentages of the samples containing them, reflecting the biases of local patterns of species abundance.


Mean annual temperature, °C
0
5
10
15
20
25
30
0
0.2
0.4
0.6
0.8
1
Proportion of entire margins
this paper
Wolfe 1979
Wolfe 1993, all
Wolfe 1993, warm

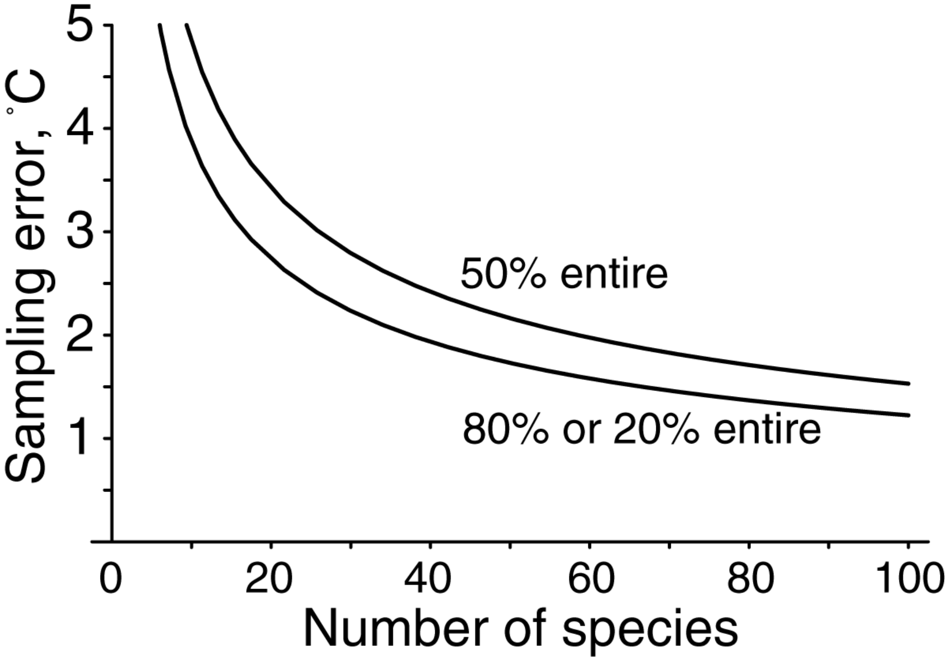
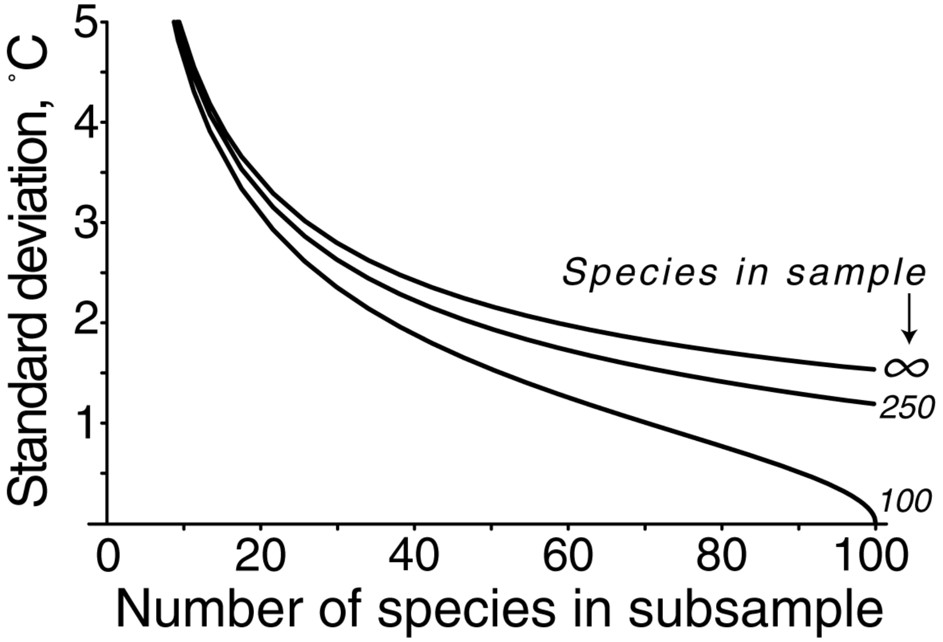

5
4
3
2
1
Sampling error, ˚C
50% entire
80% or 20% entire
0
20
40
60
80
100
Number of species

FIGURE 2.3



Standard deviation, °C
5
4
3
2
1
0
20
40
60
80
100
Number of species in subsample
Species in sample
∞
250
100

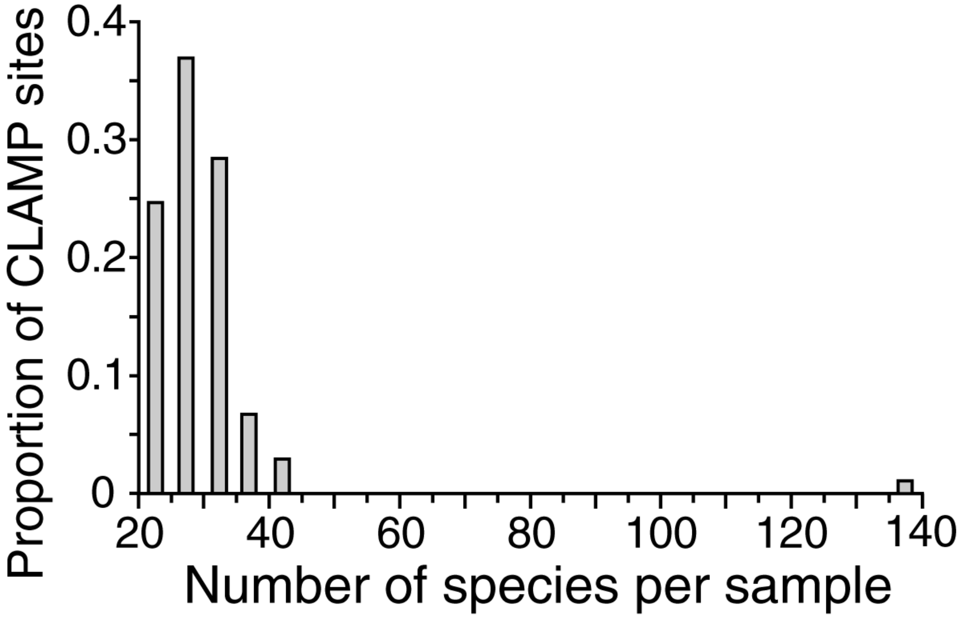

Proportion of CLAMP sites
0.4
0.3
0.2
0.1
0
20
40
60
80
100
120
140
Number of species per sample

FIGURE 2.5

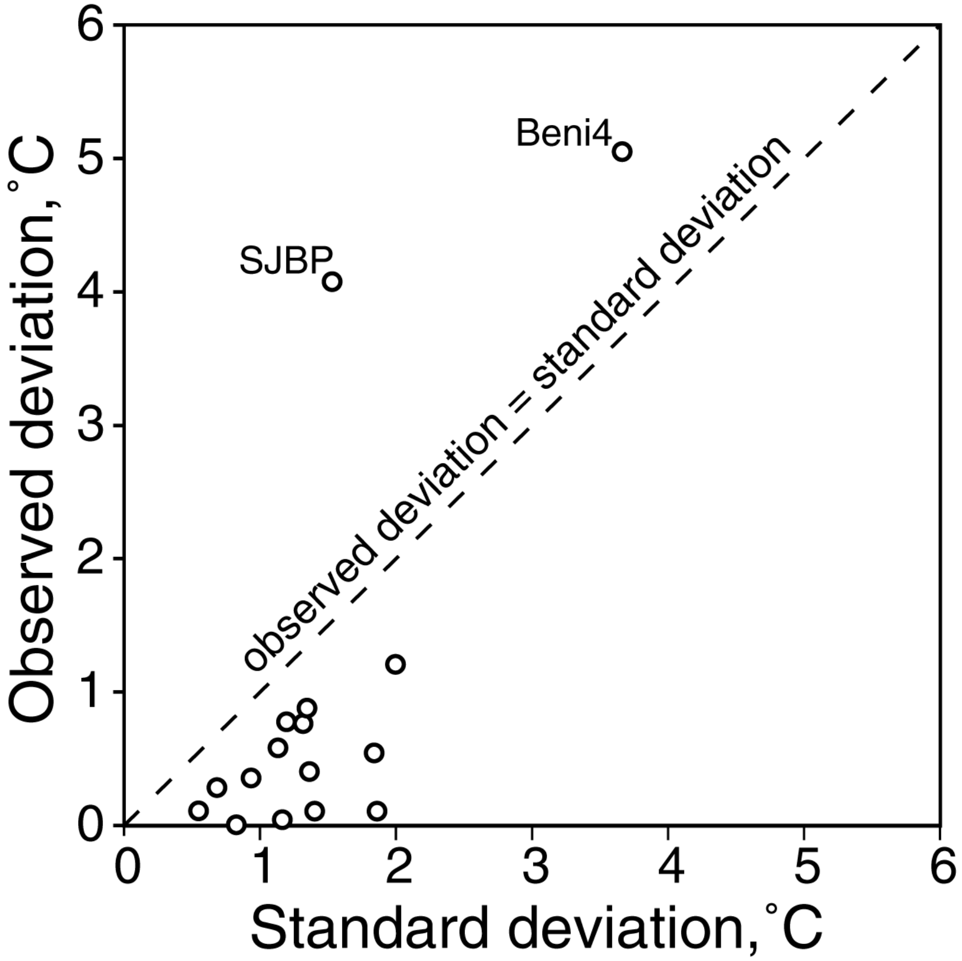
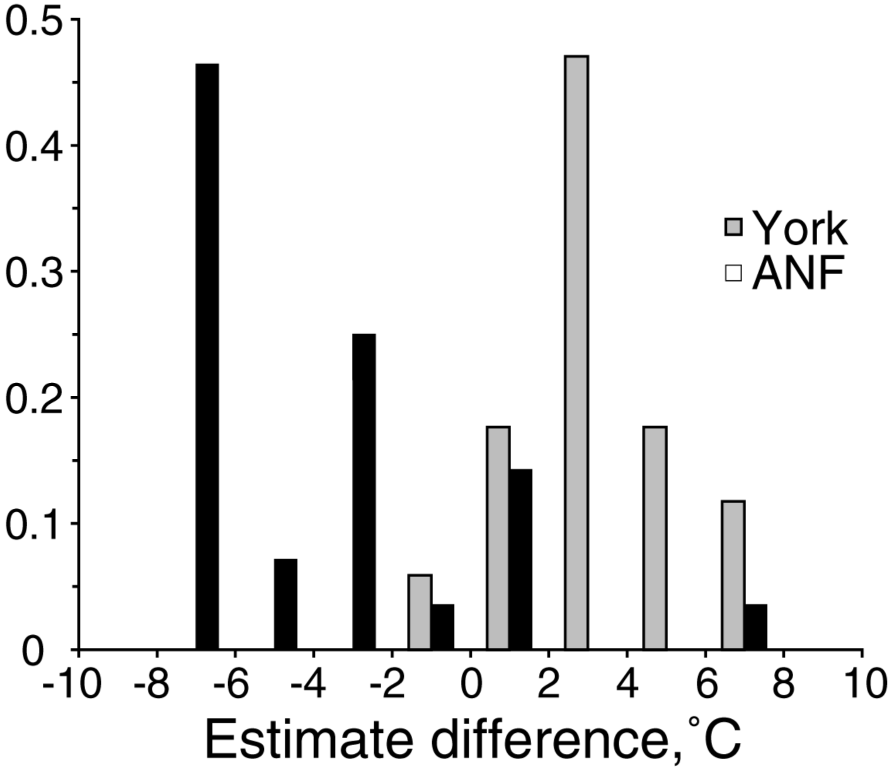

Beni4
SJBP
observed deviation = standard deviation
Observed deviation, ˚C
Standard deviation, ˚C
0
1
2
3
4
5
6
0
1
2
3
4
5
6

FIGURE 2.6


0.5
0.4
0.3
0.2
0.1
0
-10
-8
-6
-4
-2
0
2
4
6
8
10
Estimate difference,˚C
▨ York
☐ ANF

Appendix 2.1

Derivation of equation (5) and proof of its convergence to equation (1) as $m + n \to \infty$.

Given m entire and n toothed leaves, we choose r leaves. The probability Prob (m,n,r,j) that exactly j entire leaves are chosen is

$$\text{Prob}\ (m,n,r,j) = \frac{\binom{m}{j}\binom{n}{r-j}}{\binom{m+n}{r}}$$

because the right side is the number of ways of choosing j entire leaves from m, times the number of ways of choosing r - j toothed leaves from n, divided by the total number of outcomes.

Hence, the average proportion of entire leaves that will be chosen is clearly

$$\frac{m}{m+n} \quad .$$

The variance of the proportion of leaves chosen that are entire, i.e., the variance of j / r, is then

$$\sigma^2 = \sum_j \left(\frac{j}{r}\right)^2 \text{Prob}(m,\ n,\ r,\ j) - \left(\frac{m}{m+n}\right)^2$$

$$= \sum_j \frac{j^2}{r^2} \frac{\binom{m}{j}\binom{n}{r-j}}{\binom{m+n}{r}} - \left(\frac{m}{m+n}\right)^2$$

$$= \frac{mn(m+n-r)}{r(m+n)^2(m+n-1)} \quad .$$

The standard deviation of the proportion of entire leaves chosen is therefore

$$\sigma(m, n, r) = \frac{1}{m+n}\sqrt{\frac{mn(m+n-r)}{r(m+n-1)}}$$

which is equation (5).

Consider a limiting situation for the standard deviation above. Assume that *m*, the number of entire leaves, is equal to *P*(*m* + *n*) (i.e., a fixed proportion of the total number of leaves), where *P* is a fixed constant, i.e., that *m* = *Pn*/(1 - *P*). Now, let *n* → ∞. We find, from equation (5), that

$$\lim_{n\to\infty}\sigma\left(\frac{Pn}{1-P}, n, r\right) = \sqrt{\frac{P(1-P)}{r}} \quad ,$$

which is equation (1).

Appendix 2.2

Species richness, leaf-margin data, and locality information for transects. “Y” transects from York County; “M” transects from Allegheny National Forest (McKean County, Pennsylvania). Shown for each transect: transect number; location (± 2”, ± 10 m); number of species; proportion of entire-margined species; leaf-estimated mean annual temperature (LMAT) (eq. 2), °C. Actual MAT’s are 11.8°C for York County and 7.2°C for ANF (Table 2.1).

	Latitude (N), longitude (W), elevation (m)	#Species	Entire	LMAT
Y1.1	39°50'20", 76°22'27", 220	15	0.4	13.4
Y1.2	39°50'23", 76°22'27", 210	12	0.375	12.6
Y1.3	39°50'16", 76°22'30", 220	11	0.409	13.7
Y1.4	39°50'09", 76°22'29", 200	18	0.361	12.2
Y1.5	39°50'13", 76°22'27", 190	16	0.375	12.6
Y2.1	39°52’42", 76°23'02", 60	10	0.25	8.8
Y2.2	39°53'02", 76°22'53", 50	14	0.429	14.3
Y2.3	39°53'22", 76°22'54", 50	12	0.5	16.4
Y3.1	40°00'38", 76°39'23", 260	7	0.5	16.4
Y3.2	40°00'42", 76°38'54", 280	13	0.308	10.6
Y3.3	40°00'37", 76°38'59", 270	14	0.429	14.3
Y4	40°03'11", 76°36'56", 170	13	0.385	12.9
Y5	40°02'48", 76°33'40", 70	13	0.346	11.7
Y6.1	39°50'37", 76°21'22", 180	13	0.346	11.7
Y6.2	39°50'32", 76°21'16", 150	16	0.375	12.6
Y7.1	39°50'29", 76°21'08", 60	12	0.417	13.9
Y7.2	39°50'45", 76°21'05", 60	12	0.375	12.6
M1	41°51'42", 78°52'22", 650	11	0.455	15
M2.1	41°53'37", 78°53'09", 440	12	0.25	8.8
M2.2	41°54'10", 78°52'29", 450	5	0	1.1
M3.1	41°53'33", 78°53'24", 410	4	0.25	8.8
M3.2	41°53'33", 78°53'20", 410	7	0.143	5.5
M4.1	41°53'59", 78°49'33", 650	6	0.25	8.8
M4.2	41°53'59", 78°49'33", 650	6	0.25	8.8
M4.3	41°53'59", 78°49'33", 650	4	0	1.1
M5.1	41°42'25", 78°49'26", 470	7	0	1.1
M5.2	41°42'30", 78°49'18", 470	8	0.125	5.0
M5.3	41°42'33", 78°49'08", 470	6	0	1.1
M6.1	41°42'39", 78°49'38", 480	7	0.071	3.3
M6.2	41°42'39", 78°49'38", 480	6	0	1.1
M6.3	41°42'46", 78°49'22", 550	4	0	1.1
M6.4	41°42'48", 78°49'25", 580	5	0.2	7.3
M7.1	41°46'30", 78°53'01", 440	9	0.167	6.2
M7.2	41°46'29", 78°52'59", 440	12	0.125	5.0
M8.1	41°46'21", 78°51'23", 410	5	0	1.1
M8.2	41°46'43", 78°50'32", 420	10	0	1.1
M8.3	41°45'41", 78°44'11", 460	11	0	1.1

	Latitude (N), longitude (W), elevation (m)	#Species	Entire	LMAT
M8.4	41°45'41", 78°44'11", 460	8	0.125	5.0
M9.1	41°39'44", 78°55'13", 560	8	0	1.1
M9.2	41°39'20", 78°54'50", 580	4	0	1.1
M10	41°39'43", 78°53'33", 480	6	0.167	6.2
M11.1	41°52'08", 78°48'33", 540	5	0	1.1
M11.2	41°52'09", 78°48'35", 540	5	0.1	4.2
M11.3	41°52'10", 78°48'37", 540	5	0	1.1
M12	41°54'50", 78°46'15", 630	6	0.167	6.2

Appendix 2.3

Leaf-margin scores, following procedure in text, and frequencies of occurrence for leaves of species collected in 17 York County transects, *f*(York), and 28 Allegheny National Forest transects, *f*(ANF). Species scored as collected in area, resulting in one discrepancy (*Rubus idaeus*). *Rhus typhina* L. was collected at roadside in York County but not in a transect- it is included in the subsample for York County but not in this list.

Genus	*species*	Margin	*f*(York)	*f*(ANF)
Acer	*negundo* L.	0.5	6	
Acer	*pensylvanicum* L.	0		6
Acer	*rubrum* L.	0	10	12
Acer	*saccharinum* L.	0	5	
Acer	*saccharum* Marsh.	0		19
Acer	*spicatum* Lam.	0		2
Alnus	*serrulata* (Ait.) Willd.	0	1	
Amelanchier	*laevis* Wieg.	0	1	1
Amorpha	*fruticosa* L.	1	2	
Aronia	*arbutifolia* (L.) Ell.	0	1	
Asimina	*triloba* (L.) Dunal	1	8	
Betula	*lenta* L.	0	6	1
Betula	*nigra* L.	0	2	
Carpinus	*caroliniana* (Walt.)	0		17
Carya	*cordiformis* (Wang.) K. Koch	0	2	
Carya	*glabra* (Mill.) Sweet	0	5	
Carya	*laciniosa* (Michx.) Loud	0	2	
Carya	*ovalis* (Wang.) Sarg.	0	2	
Carya	*ovata* (Mill.) K. Koch	0	1	1
Carya	*tomentosa* Nutt.	0	4	
Castanea	*dentata* (Marsh.) Borkh.	0	3	
Celtis	*occidentalis* L.	0	2	
Clematis	*virginiana* L.	0		3
Comptonia	*peregrina* (L.) Coult.	1		1
Cornus	*amomum* Mill.	1	4	4
Cornus	*florida* L.	1	1	
Crataegus	sp.	0		1
Dirca	*palustris* L.	1		1
Fagus	*grandifolia* Ehrh.	0	7	24
Fraxinus	*americana* L.	0.5	6	6
Hamamelis	*virginiana* L.	0	1	4
Hydrangea	*arborescens* L.	0	1	
Ilex	*verticillata* (L.) Gray	0	1	
Kalmia	*latifolia* L.	1	4	1
Lindera	*benzoin* (L.) Blume	1	13	
Liriodendron	*tulipifera* L.	1	15	1
Magnolia	*acuminata* L.	1		6
Nyssa	*sylvatica* Marsh.	1	1	

Genus	*species*	Margin	*f*(York)	*f*(ANF)
Ostrya	*virginiana* (Mill.) K. Koch	0		1
Parthenocissus	*quinquefolia* (L.) Planch	0	1	
Platanus	*occidentalis* L.	0	5	
Populus	*grandidentata* Michx.	0	1	3
Populus	*tremuloides* Michx.	0		3
Prunus	*serotina* Ehrh.	0	8	23
Prunus	*virginiana* L.	0		1
Quercus	*alba* L.	1	5	1
Quercus	*coccinea* Muenchh.	0	10	
Quercus	*prinus* L.	0	9	1
Quercus	*rubra* L.	0	2	5
Quercus	*velutina* Lam.	0.5	6	
Rhododendron	*maximum* L.	1		1
Rhododendron	*nudiflorum* (L.) Torr.	1	1	
Rhus	*typhina* L.	0		2
Robinia	*pseudo-acacia* L.	1	4	
Rubus	*allegheniensis* Porter	0	10	5
Rubus	*idaeus* L.	0.5	5	
Rubus	*idaeus* L.	0		4
Rubus	*occidentalis* L.	0		1
Rubus	sp.	0	2	
Salix	*discolor* Muhl.	0		2
Salix	*eriocephala* Michx.	0		1
Salix	*lucida* Muhl.	0		1
Salix	*nigra* Marsh.	0	4	1
Salix	*sericea* Marsh.	0		6
Salix	sp.	0	2	
Sambucus	*canadensis* L.	0	1	1
Sambucus	*pubens* Michx.	0		1
Sassafras	*albidum* (Nutt.) Nees	1	11	1
Smilax	*rotundifolia* L.	1	4	
Tilia	*americana* L.	0	1	6
Ulmus	*americana* L.	0	4	4
Ulmus	*rubra* Muhl.	0		2
Vaccinium	*angustifolium* Ait.	0		1
Vaccinium	*corymbosum* L.	0.5	1	
Vaccinium	*myrtilloides* Michx.	1		1
Viburnum	*acerifolium* L.	0	3	
Viburnum	*cassinoides* L.	1		1
Viburnum	*recognitum* Fern.	0	2	1
Vitis	*aestivalis* Michx.	0	1	
Vitis	*vulpina* L.	0	7	

Appendix 2.4

Presence-absence data for York County transects. Transect names and locations as in Appendix 2.2.

Transect Y-	**1.1**	**1.2**	**1.3**	**1.4**	**1.5**	**2.1**	**2.2**	**2.3**	**3.1**	**3.2**	**3.3**	**4**	**5**	**6.1**	**6.2**	**7.1**	**7.2**
Acer negundo	0	0	1	0	0	1	1	1	0	0	0	0	1	0	0	1	0
Acer rubrum	1	0	1	1	1	0	0	0	1	1	1	0	0	1	1	0	1
Acer saccharinum	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	0
Alnus serrulata	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Amelanchier laevis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Amorpha fruticosa	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Aronia arbutifolia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Asimina triloba	0	1	0	1	0	0	1	1	0	0	0	1	0	1	0	1	1
Betula lenta	0	0	1	1	0	0	0	0	0	0	0	1	1	0	1	0	1
Betula nigra	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Carya cordiformis	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Carya glabra	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Carya laciniosa	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Carya ovalis	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Carya ovata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Carya tomentosa	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Castanea dentata	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1
Celtis occidentalis	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Cornus amomum	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1
Cornus florida	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Fagus grandifolia	0	1	0	0	1	1	1	0	0	0	0	0	0	1	1	1	0
Fraxinus americana	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1
Hamamelis virginiana	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Hydrangea arborescens	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ilex verticillata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Kalmia latifolia	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0
Lindera benzoin	1	1	1	1	1	1	1	1	0	0	1	0	1	0	1	1	1
Liriodendron tulipifera	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1	1
Nyssa sylvatica	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parthenocissus quinquefolia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Platanus occidentalis	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	0
Populus grandidentata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Prunus serotina	1	0	0	1	1	0	1	0	1	1	1	0	0	1	0	0	0
Quercus alba	0	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	0
Quercus coccinea	0	0	1	1	1	1	0	0	0	0	1	1	0	1	1	1	1
Quercus prinus	0	0	0	1	0	1	0	0	1	1	1	1	0	1	1	0	1
Quercus rubra	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Quercus velutina	0	0	1	1	1	0	0	0	1	1	0	0	0	0	1	0	0
Rhododendron nudiflorum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Robinia pseudo-acacia	1	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0

Transect Y-	**1.1**	**1.2**	**1.3**	**1.4**	**1.5**	**2.1**	**2.2**	**2.3**	**3.1**	**3.2**	**3.3**	**4**	**5**	**6.1**	**6.2**	**7.1**	**7.2**
Rubus allegheniensis	1	1	1	1	1	0	0	0	0	1	1	1	0	1	1	0	0
Rubus idaeus	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Rubus "sp. 3"	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix nigra	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0
Salix "sp. 2"	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Sambucus canadensis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sassafras albidum	1	1	1	1	1	0	0	0	1	0	1	1	0	1	1	1	0
Smilax rotundifolia	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0
Tilia americana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ulmus americana	0	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0
Vaccinium corymbosum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Viburnum acerifolium	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Viburnum recognitum	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Vitis vulpina	1	1	1	1	0	0	1	1	0	0	0	0	1	0	0	0	0
Vitis aestivalis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 2.5

Presence-absence data for Allegheny National Forest transects. Transect names and locations as in Appendix 2.2.

Transect M-	**1**	**2.1**	**2.2**	**3.1**	**3.2**	**4.1**	**4.2**	**4.3**	**5.1**	**5.2**	**5.3**	**6.1**	**6.2**	**6.3**	**6.4**	**7.1**	**7.2**	**8.1**
Acer pennsylvanicum	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
Acer rubrum	1	0	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1
Acer saccharum	0	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1
Acer spicatum	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Amelanchier laevis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Betula lenta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carpinus caroliniana	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1
Carya ovata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clematis virginiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Comptonia peregrina	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornus amomum	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0
Crataegus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dirca palustris	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fagus grandifolia	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Fraxinus americana	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	1	1	0
Hamamelis virginiana	1	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Kalmia latifolia	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liriodendron tulipifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magnolia acuminata	1	1	0	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0
Ostrya virginiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Populus grandidentata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Populus tremuloides	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0
Prunus serotina	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1
Prunus virginiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Quercus alba	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Quercus prinus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Quercus rubra	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0
Rhododendron maximum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhus typhina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Rubus allegheniensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Rubus idaeus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus occidentalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Salix discolor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix eriocephala	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix lucida	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix nigra	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Salix sericea	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sambucus canadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sambucus pubens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sassafras albidum	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Transect M-	**1**	**2.1**	**2.2**	**3.1**	**3.2**	**4.1**	**4.2**	**4.3**	**5.1**	**5.2**	**5.3**	**6.1**	**6.2**	**6.3**	**6.4**	**7.1**	**7.2**	**8.1**
Tilia americana	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Ulmus americana	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Ulmus rubra	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Vaccinium angustifolium	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium myrtilloides	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum cassinoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum recognitum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Transect M-	**8.2**	**8.3**	**8.4**	**9.1**	**9.2**	**10**	**11.1**	**11.2**	**11.3**	**12**
Acer pennsylvanicum	0	0	0	1	0	0	0	0	0	1
Acer rubrum	1	1	0	1	1	0	0	0	0	0
Acer saccharum	0	1	0	0	1	0	1	1	1	1
Acer spicatum	0	0	0	0	0	0	0	0	0	0
Amelanchier laevis	0	0	0	0	0	0	0	0	0	0
Betula lenta	0	0	0	0	0	0	0	0	0	0
Carpinus caroliniana	1	1	0	1	0	1	1	0	1	1
Carya ovata	0	0	0	0	0	0	0	0	0	0
Clematis virginiana	1	1	1	0	0	0	0	0	0	0
Comptonia peregrina	0	0	0	0	0	0	0	0	0	0
Cornus amomum	0	0	0	0	0	0	0	0	0	0
Crataegus sp.	1	0	0	0	0	0	0	0	0	0
Dirca palustris	0	0	0	0	0	0	0	0	0	0
Fagus grandifolia	1	1	0	1	1	0	1	1	1	1
Fraxinus americana	0	0	0	0	0	0	0	1	0	0
Hamamelis virginiana	0	0	0	0	0	0	0	0	0	0
Kalmia latifolia	0	0	0	0	0	0	0	0	0	0
Liriodendron tulipifera	0	0	0	0	0	0	0	0	0	1
Magnolia acuminata	0	0	0	0	0	0	0	0	0	0
Ostrya virginiana	0	0	0	1	0	0	0	0	0	0
Populus grandidentata	1	0	0	0	0	0	0	0	0	0
Populus tremuloides	0	0	0	0	0	0	0	0	0	0
Prunus serotina	0	1	1	1	1	1	1	1	1	1
Prunus virginiana	1	0	0	0	0	0	0	0	0	0
Quercus alba	0	0	0	0	0	0	0	0	0	0
Quercus prinus	0	0	0	0	0	0	0	0	0	0
Quercus rubra	0	0	0	0	0	0	0	0	0	0
Rhododendron maximum	0	0	1	0	0	0	0	0	0	0
Rhus typhina	0	0	1	0	0	0	0	0	0	0
Rubus allegheniensis	1	1	0	1	0	1	0	0	0	0
Rubus idaeus	1	1	1	0	0	1	0	0	0	0
Rubus occidentalis	0	0	0	0	0	0	0	0	0	0
Salix discolor	0	1	1	0	0	0	0	0	0	0

Transect M-	**8.2**	**8.3**	**8.4**	**9.1**	**9.2**	**10**	**11.1**	**11.2**	**11.3**	**12**
Salix eriocephala	0	0	0	0	0	0	0	0	0	0
Salix lucida	0	0	0	0	0	0	0	0	0	0
Salix nigra	0	0	0	0	0	0	0	0	0	0
Salix sericea	1	1	1	0	0	1	0	0	0	0
Sambucus canadensis	0	1	0	0	0	0	0	0	0	0
Sambucus pubens	0	0	0	1	0	0	0	0	0	0
Sassafras albidum	0	0	0	0	0	0	0	0	0	0
Tilia americana	0	0	0	0	0	0	1	1	1	0
Ulmus americana	0	0	1	0	0	0	0	0	0	0
Ulmus rubra	0	0	0	0	0	0	0	0	0	0
Vaccinium angustifolium	0	0	0	0	0	0	0	0	0	0
Vaccinium myrtilloides	0	0	0	0	0	0	0	0	0	0
Viburnum cassinoides	0	0	0	0	0	1	0	0	0	0
Viburnum recognitum	0	0	0	0	0	0	0	0	0	0

Appendix 2.6

Complete leaf-margin data set, showing margin type, scored as in text, and sample(s) where found (Table 2.1). BE: Beni Biodiversity plots; M: Manu Biodiversity Plots; BC: Barro Colorado Island; BI: Bisley Watersheds; G: Guánica Commonwealth Forest; SD: St. John, dry woodland; SM: St. John, moist forest; Y: York County, Pennsylvania; A: Allegheny National Forest, Pennsylvania. Nomenclature as in the cited references in text; see these references for authorities. However, where two or more samples contain the same species under different names, I have listed only the more recent name below.

Species	Margin; sample(s)
ACANTHACEAE	
Aphelandra sinclairiana	1; BC
Justicia carthaginensis	1; SD
Justicia graciliflora	1; BC
Oplonia microphylla	1; SM
Oplonia spinosa	1; SM
Ruellia tweediana	1; SM
Trichanthera gigantea	1; BC
ACERACEAE	
Acer negundo	0.5; Y
Acer pennsylvanicum	0; A,Y
Acer rubrum	0; A,Y
Acer saccharinum	0; Y
Acer saccharum	0; A,Y
Acer spicatum	0; A,Y
ANACARDIACEAE	
Anacardium excelsum	1; BC
Astronium graveolens	0; BC,M
Comocladia dodonaea	1; G,SD,SM
Comocladia glabra	1; BI
Mosquitoxylum jamaicense	1; BC
Rhus copallina	1; A,Y
Rhus glabra	0; Y
Rhus typhina	0; A,Y
Spondias mombin	1; BC,BE,BI, M, SD,SM
Spondias radlkoferi	1; BC
Tapirira peckoltiana cf.	1; M
Toxicodendron radicans	0.5; Y
1	0; BE
2	1; BE
ANNONACEAE	
Anaxagorea panamensis	1; BC
Annona acuminata	1; BC
Annona glabra	1; BC,SM
Annona hayesii	1; BC
Annona hypoglauca	1; M
Annona muricata	1; SD,SM
Annona reticulata	1; G,BI
Annona spraguei	1; BC
Annona squamosa	1; SM
Cremastosperma sp.	1; BC
Desmopsis panamensis	1; BC
Duguetia 12711	1; M
Duguetia quitarensis	1; M
Duguetia spixiana	1; M

Species	Margin; sample(s)
Guatteria acutissima'	1; M
Guatteria amplifolia	1; BC
Guatteria caribaea	1; BI
Guatteria dumetorum	1; BC
Guatteria sp.	1; BE
Malmea diclina	1; M
Malmea dielsiana	1; M
Oxandra mediocris	1; M
Porcelia nitida	1; M
Rollinia pittieri	1; M
Rollinia sp.	1; BE
Ruizodendron ovale	1; M
Trigynaea duckei	1; M
Unonopsis floribunda	1; M
Unonopsis mathewsii	1; BE,M
Unonopsis pittieri	1; BC
Xylopia benthamii	1; M
Xylopia frutescens	1; BC
Xylopia ligustrifolia	1; BE,M
Xylopia macrantha	1; BC
APOCYNACEAE	
Allamanda cathartica	1; BI,BC
Aspidosperma 13158	1; M
Aspidosperma cruenta	1; BC
Aspidosperma megalocarpon	1; BC
Aspidosperma megaphyllum	1; M
Aspidosperma rigidum	1; BE
Aspidosperma vargasii	1; M
Forsteronia myriantha	1; BC
Forsteronia peninsularis	1; BC
Forsteronia portoricensis	1; BI
Forsteronia viridescens	1; BC
Himatanthus sucuuba	1; M
Lacmellea panamensis	1; BC
Malouetia guatemalensis	1; BC
Mandevilla villosa	1; BC
Mesechites trifida	1; BC
Odontadenia macrantha	1; BC
Odontadenia puncticulosa	1; BC
Plumeria alba	1; G,SD
Prestonia acutifolia	1; BC
Prestonia ipomaeifolia	1; BC
Prestonia obovata	1; BC
Prestonia portobellensis	1; BC

Species	Margin; sample(s)
Rauvolfia nitida	1; G,SD,SM
Rauvolfia viridis	1; SD,SM
Rhabdadenia biflora	1; BC
Stemmadenia grandiflora	1; BC
Tabernaemontana arborea	1; BC
Tabernaemontana psychotriaefolia	1; M
Tabernaemontana sp.	1; BE
Thevetia ahouai	1; BC
AQUIFOLIACEAE	
Ilex montana	0; A
Ilex nitida	0; G
Ilex urbanii	1; SM
Ilex verticillata	0; Y
ARALIACEAE	
Dendropanax arboreus	1; BC,BE,BI
Dendropanax stenodontus	0; BC
Didymopanax morototoni	1; BC,BE,BI,SM
Oreopanax capitatus	1; BC
ARISTOLOCHIACEAE	
Aristolochia chapmaniana	1; BC
Aristolochia odoratissima	1; SM
Aristolochia trilobata	1; SM
ASCLEPIADACEAE	
Cynanchum cubense	1; BC
Cynanchum recurvum	1; BC
Marsdenia crassipes	1; BC
Matelea maritima	1; SM
Metastelma (Cynanchum) griesebachianum	1; SD
ASTERACEAE	
Calea prunifolia	0; BC
Chromolaena odorata	0; BC, BI, SM
Clibadium asperum	0; BC
Clibadium erosum	0; BI
Clibadium surinamense	0; BC
Heterocondylus vitalbis	0; BC
Koanophyllon wetmorei	0; BC
Mikania cordifolia	0; BI,SM
Mikania fragilis	0; BI
Mikania leiostachya	1; BC
Mikania tonduzii	1; BC
Pluchea carolinensis	1; SM
Vernonia albicaulis	1; SD,SM

Species	Margin; sample(s)
Vernonia canescens	0.5; BC
Vernonia patens	0; BC
Wedelia calycina	0; SM
Wulffia baccata	0; BC
BETULACEAE	
Alnus serrulata	0; Y
Betula allegheniensis	0; A,Y
Betula lenta	0; A,Y
Betula nigra	0; Y
Carpinus caroliniana	0; A,Y
Corylus americana	0; Y
Corylus cornuta	0; Y
Ostrya virginiana	0; A,Y
BIGNONIACEAE	
Adenocalymma apurense	1; BC
Adenocalymma arthropetiolatum	1; BC
Amphilophium paniculatum	1; BC
Anemopaegma chrysoleucum	1; BC
Arrabidaea florida	1; BC
Arrabidaea candicans	1; BC
Arrabidaea chica	1; BC
Arrabidaea patellifera	1; BC
Arrabidaea verrucosa	1; BC
Arrabidaea chica	1; SM
Callichlamys latifolia	1; BC
Ceratophytum tetragonolobum	1; BC
Clytostoma binatum	1; BC
Crescentia cujete	1; SD,SM
Crescentia linearifolia	1; G
Cydista aequinoctalis	1; BC,SM
Cydista heterophylla	1; BC
Enallagma latifolia	1; G,SM
Jacaranda copaia	0.5; BC,M
Macfadyena unguis-cati	1; BC,SD,SM
Martinella obovata	1; BC
Pachyptera kerere	1; BC
Paragonia pyramidata	1; BC
Phryganocydia corymbosa	1; BC
Pithecoctenium crucigerum	1; BC
Pleonotoma variabilis	1; BC
Spathodea campanulata	1; SD,SM

Species	Margin; sample(s)
Stizophyllum riparium	0.5; BC
Tabebuia aurea	1; BE
Tabebuia guayacan	1; BC
Tabebuia heptaphylla	0; BE
Tabebuia heterophylla	1; BI,G,SD,SM
Tabebuia impetiginosa	1; M
Tabebuia ochracea	0.5; BC
Tabebuia rosea	1; BC
Tabebuia roseo-alba	1; BE
Tabebuia serratifolia	0; M
Tecoma stans	0; SD
Tynnanthus croatianus	1; BC
Xylophragma seemannianum	1; BC
BIXACEAE	
Bixa orellana	1; BC
Bixa platycarpa	1; M
BOMBACACEAE	
Bombacopsis quinata	1; BC
Bombacopsis sessilis	1; BC
Cavanillesia platanifolia	1; BC
Ceiba pentandra	1; BC,SD,SM
Ceiba samauma	1; BE,M
Chorisia insignis	1; M
Huberodendron swietenioides	1; M
Matisia cordata	1; M
Ochroma lagopus	1; BI
Ochroma pyramidale	1; BC
Pachira aquatica	1; BC
Pseudobombax longiflorum	1; BE
Pseudobombax marginatum	1; BE
Pseudobombax septenatum	1; BC,M
Quararibea asterolepis	1; BC,
Quararibea ochrocalyx	1; M
Quararibea pterocalyx	1; BC
Quararibea turbinata	1; BI,SM
Quararibea wittii	1; M
BORAGINACEAE	
Bourreria succulenta	1; G,SD,SM
Bourreria virgata	1; G
Cordia 2	BE
Cordia 12752	1; M

Species	Margin; sample(s)
Cordia alliodora	1; BC,BE,SD,SM
Cordia bicolor	1; BC
Cordia borinquensis	1; BI
Cordia collococca	1; G,SD,SM
Cordia laevigata(nitida)	1G,; SD,SM
Cordia lasiocalyx	1; BC
Cordia nodosa	1; M
Cordia panamensis	1; BC
Cordia polycephala	0; SM
Cordia rickseckeri	1; G
Cordia spinescens	0; BC
Cordia sulcata	0; BI,SD,SM
Rochefortia acanthophora	1; G
Tournefortia angustiflora	1; BC
Tournefortia bicolor	1; BC,SM
Tournefortia cuspidata	1; BC
Tournefortia filiflora	1; SM
Tournefortia hirsutissima	1; BC,SM
Tournefortia microphylla	1; SD,SM
BURSERACEAE	
Bursera simaruba	1; BC,G,SD,SM
Dacryodes excelsa	1; BI
Protium costaricense	1; BC
Protium panamense	1; BC
Protium tenuifolium	1; BC
Tetragastris altissima	1; M
Tetragastris balsamifera	1; BI,G
Tetragastris panamensis	1; BC
Trattinnickia 12703	1; M
Trattinnickia aspera	1; BC
Trattinnickia peruviana	1; M
CANELLACEAE	
Canella winterana	1; G,SD
CAPPARIDACEAE	
Capparis amplissima	1; G,SD,SM
Capparis cynophallophora	1; G,SD,SM
Capparis flexuosa	1; G,SD,SM
Capparis frondosa	1; BC,G,SD,SM
Capparis hastata	1; G,SD,SM
Capparis indica	1; G,SD,SM
Capparis macrophylla'	1; M
Capparis nitida	1; M

Species	Margin; sample(s)
Crataeva benthamii	1; M
Morisonia americana	1; G,SD,SM
CAPRIFOLIACEAE	
Diervilla lonicera	0; A,Y
Lonicera dioica	1; A
Sambucus canadensis	0; A,Y
Sambucus racemosa	0; Y
Viburnum acerifolium	0; Y
Viburnum cassinoides	0.5; A,Y
Viburnum dentatum	0; Y
Viburnum lantanoides	0; A
Viburnum prunifolium	0; Y
Viburnum recognitum	0; A,Y
CARICACEAE	
Carica cauliflora	0; BC
Jacaratia digitata	1; M
Jacaratia spinosa	1; BC
CARYOCARACEAE	
Caryocar amygdaliforme	0; M
CELASTRACEAE	
Cassine xylocarpa	0.5; G,SD,SM
Celastrus scandens	0; Y
Crossopetalum rhacoma	0; G,SD,SM
Euonymus americanus	0; Y
Gyminda latifolia	1; G
Maytenus ebenifolia	0; BE
Maytenus elliptica	1; SD,SM
Maytenus schippii	1; BC
Schaefferia frutescens	1; G,SD
CHLORANTHACEAE	
Hedyosmum arborescens	0; BI
CHRYSOBALANACEAE	
Hirtella americana	1; BC
Hirtella excelsa	1; M
Hirtella racemosa	1; BC
Hirtella rugosa	1; BI
Hirtella triandra	1; BC,BE,BI,M
Licania britteniana	1; M
Licania hypoleuca	1; BC,M
Licania hypoleuca	1; M
Licania platypus	1; BC
Licania silvae	1; M
Parinari klugii	1; M
CLUSIACEAE	
Ascyrum hypericoides	1; Y
Calophyllum brasiliense	1; BI,BE,M

Species	Margin; sample(s)
Calophyllum longifolium	1; BC
Chrysochlamys ulei	1; M
Clusia clusioides	1; BI
Clusia gundlachii	1; BI
Clusia odorata	1; BC
Clusia rosea	1; G,SD,SM
Garcinia acuminata	1; BC, M
Garcinia brasiliensis cf	1; M
Garcinia brasiliensis	1; BE
Garcinia edulis	1; BC
Garcinia portoricensis	1; BI
Havetiopsis flexilis	1; BC
Hypericum densiflorum	1; Y
Hypericum prolificum	1; Y
Mammea americana	1; SM
Marila laxiflora	1; BC
Symphonia globulifera	1; BC,BE,M
Tovomita longifolia	1; BC
Tovomita stylosa	1; BC
Tovomitopsis nicaraguensis	1; BC
Vismia baccifera	1; BC
Vismia billbergiana	1; BC
Vismia gracilis	1; M
Vismia macrophylla	1; BC
Vismia sprucei	1; M
COCHLOSPERMACEAE	
Cochlospermum vitifolium	0; BC
COMBRETACEAE	
Buchenavia capitata	1; BI,SM
Bucida buceras	1; G,SD,SM
Combretum casoucia	1; BC
Combretum decandrum	1; BC
Combretum fruticosum	1; BC
Combretum laxum	1; BC
Conocarpus erectus	1; G,SD,SM
Laguncularia racemosa	1; G
Terminalia amazonica	1; BC.M
Terminalia catappa	1; SM
Terminalia chiriquensis	1; BC
Terminalia oblonga	1; BE,M
CONNARACEAE	
Cnestidium rufescens	1; BC
Connarus panamensis	1; BC
Connarus turczaninowii	1; BC
Rourea glabra	1; BC
Rourea surinamensis	1; BI

Species	Margin; sample(s)
CONVOLVULACEAE	
Convolvulus nodiflorus	1; SD
Ipomoea eggersii	1; SD
Ipomoea macrantha	1; SM
Ipomoea nil	1; SM
Ipomoea phillomega	1; BC
Ipomoea setifera	1; BI
Ipomoea tiliacea	1; BI
Iseia luxurians	1; BC
Jacquemontia pentanthos	1; SD
Maripa panamensis	1; BC
Merremia aegypta	1; SM
Merremia dissecta	1; SM
Merremia umbellata	1; SM
Stictocardia tilliifolia	1; SM
CORNACEAE	
Cornus alternifolia	1; A,Y
Cornus amomum	1; A,Y
Cornus florida	1; Y
Cornus racemosa	1; Y
CUCURBITACEAE	
Cayaponia granatensis	1; BC
Cayaponia racemosa	1; BI
Corallocarpus emetocatharticus	0; SD
Fevillea cordifolia	0.5; BC
Gurania coccinea	0; BC
Gurania makoyana	0; BC
Gurania megistantha	0; BC
CUCURBITACEAE	
Psiguria bignoniacea	0.5; BC
DICHAPETALACEAE	
Tapura juruana	1; M
DILLENIACEAE	
Curatella americana	0; BE
Davilla nitida	0.5; BC
Doliocarpus dentatus	0.5; BC
Doliocarpus major	0.5; BC
Doliocarpus multiflorus	1; BC
Doliocarpus olivaceus	0.5; BC
Pinzona coriacea	1; BI
Saurauia laevigata	0; BC
Tetracera portobellensis	1; BC
Tetracera volubilis	0.5; BC
EBENACEAE	
Diospyros artanthifolia	1; BC
Diospyros subrotata	1; M
ELAEOCARPACEAE	
Muntingia calabura	0; BC
Sloanea 2034	1; M
Sloanea berteriana	1; BI
Sloanea fragrans	0; M
Sloanea guianensis	1; BE,M
Sloanea sinemariensis	1; M
Sloanea terniflora	1; BC
Sloanea zuliaensis	0; BC
ERICACEAE	
Epigaea ripens	1; A,Y
Gaultheria procumbens	0; A,Y
Gaylussacia baccata	1; Y
Gaylussacia dumosa	1; Y
Kalmia latifolia	1; A,Y
Leucothoë racemosa	0; Y
Lyonia ligustrina	0.5; Y
Rhododendron arborescens	1; Y
Rhododendron atlanticum	1; Y
Rhododendron maximum	1; A,Y
Rhododendron nudiflorum	1; Y
Rhododendron periclymenoides	1; Y
Rhododendron prinophyllum	1; Y
Vaccinium angustifolium	0; A,Y
Vaccinium corymbosum	1; Y
Vaccinium myrtilloides	1; A
Vaccinium pallidum	0; Y
Vaccinium stamineum	1; Y
ERYTHROXYLACEAE	
Erythroxylum areolatum	1; G
Erythroxylum brevipes	1; SD,SM
Erythroxylum multiflorum	1; BC
Erythroxylum panamense	1; BC
Erythroxylum rotundifolium	1; G
Erythroxylum sp.	1; BE
EUPHORBIACEAE	
Acalypha diversifolia	0; BC
Acalypha macrostachya	0; BC
Acalypha mapirensis	0; M
Adelia ricinella	1; G,SD,SM
Adelia triloba	1; BC
Alchornea costaricensis	0; BC

Species	Margin; sample(s)
Alchornea glandulosa	0; M
Alchornea latifolia	0; BC,BI
Alchorneopsis floribunda	0; BI
Argythamnia fasciculata	1; SD
Bernardia dichotoma	0; G
Chamaesyce articulata	1; G
Croton astroites	1; G,SD,SM
Croton billbergianus	0.5; BC
Croton matourensis	1; M
Croton panamensis	1; BC
Croton poecilanthus	1; BI
Croton rigidus	1; G,SD
Croton tessmannii	1; M
Drypetes 1813	1; M
Drypetes alba	0; SM
Drypetes amazonica	0; M
Drypetes glauca	1; BI
Drypetes sp.	0.5; BE
Drypetes standleyi	1; BC
Euphorbia petiolaris	1; G,SD
Garcia nutans	1; BC
Glycydendron amazonicum	1; M
Gymnanthes lucida	0; G, SD, SM
Hippomane mancinella	0; G,SD,SM
Hura crepitans	0; BC,BE,SM
Hyeronima alchorneoides	1; M
Hyeronima laxiflora	1; BC
Mabea maynensis	0; M
Mabea occidentalis	0.5; BC
Margaritaria nobilis	1; BC,M,SD,SM
Omphalea diandra	1; BC
Pausandra trianae	0; M
Pera benensis	1; BE
Phyllanthus acuminatus	1; BC
Sagotia racemosa	1; M
Sapium aereum	1; M
Sapium aucuparium	0.5; BC
Sapium caribaeum	0.5; SM
Sapium caudatum	0; BC
Sapium ixiamasense	1; M
Sapium laurocerasum	1; BI
Sapium marmieri	1; BE,M
Savia sessiliflora	1; G,SD,SM
Securinega acidoton	1; G
FABACEAE	
Abrus precatorius	1; SM
Acacia acanthophylla	1; BC
Acacia glomerosa	1; BC
Acacia hayesii	1; BC
Acacia loretensis	1; BE,M
Acacia macracantha	1; SD,SM
Acacia melanoceras	1; BC
Acacia muricata	1; SD,SM
Acacia riparia	1; SM,BC
Acacia tortuosa	1; SD,SM
Adenopodia polystachya	1; BC
Aeschenomene americana	1; SM
Albizia guachepele	1; BC
Albizia niopoides	1; BE
Amorpha fruticosa	1; Y
Andira inermis	1; M,BC,G,SD,SM,BE,BI
Apuleia leiocarpa	1; M
Bauhinia guianensis	1; BC
Bauhinia reflexa	1; BC
Brownea macrophylla	1; BC
Caesalpinia bonduc	1; SD
Caesalpinia divergens	1; SD
Calliandra (Zapoteca) portoricensis	1; SD,SM
Cassia obtusifolia	1; SM
Cassia occidentalis	1; SD,SM
Cassia polyphylla	1; G
Cassia reticulata	1; BC
Cassia siamea	1; SM
Cassia undulata	1; BC
Cassia fruticosa	1; BC
Cedrelinga catenaeformis	1; M
Centrosema virginianum	1; SD,SM
Chamaecrista glandulosa	1; SD,SM
Chamaecrista sp.	1; G
Clitoria javitensis	1; BC
Copaïfera reticulata	1; BE,M
Cracca caribaea	1; SD,SM
Crotalaria falcata	1; SM
Crotalaria incana	1; SD,SM
Crotalaria lotifolia	1; SD
Cymbosema roseum	1; BC
Cynometra bauhiniaefolia	1; BC
Dalbergia brownei	1; BC

Species	Margin; sample(s)
Dalbergia monetaria	1; BC
Dalbergia retusa	1; BC
Desmodium mollis	1; SM
Dioclea guianensis	1; BC
Dioclea reflexa	1; BC
Dioclea wilsonii	1; BC
Dipteryx micrantha	1; M
Dipteryx panamensis	1; BC
Dussia tessmannii	1; M
Entada monostachya	1; BC
Enterolobium cyclocarpum	1; BC,M
Enterolobium schomburgkii	1; BC
Erythrina costaricensis	1; BC
Erythrina eggersii	1; SD,SM
Erythrina fusca	1; BC
Galactia striata	1; SD
Hymenaea courbaril	1; BC,SD,SM
Indigofera suffruticosa	1; SM
Inga 3	1; BE
Inga 1817	1; M
Inga 1975	1; M
Inga 1983	1; M
Inga 1997	1; M
Inga acreana	1; M
Inga alba	1; M
Inga calantha cf	1; M
Inga capitata	1; M
Inga chartacea	1; M
Inga ciliata	1; M
Inga cinnamomea	1; BE
Inga cocleensis	1; BC
Inga densiflora cf	1; M
Inga edulis	1; BE
Inga goldmanii	1; BC
Inga hayesii	1; BC
Inga laurina	1; G,BC,BI,SD,SM
Inga marginata	1; BC,M
Inga minutula	1; BC
Inga mucuna	1; BC
Inga multijuga	1; BC
Inga nitida	1; M
Inga nobilis	1; M
Inga pauciflora	1; BC

Species	Margin; sample(s)
Inga pezizifera	1; BC
Inga punctata	1; BC,M
Inga quaternata	1; BC
Inga ruiziana	1; BC,M
Inga sapindoides	1; BC
Inga sp.	1; M
Inga spectabilis	1; BC
Inga striata cf	1; M
Inga thibaudiana	1; BC,M
Inga umbellifera	1; BC
Inga vera	1; BI
Lecointea amazonica	1; M
Leucaena glauca	1; G,SM
Leucaena leucocephala	1; SD,SM
Leucaena multicapitula	1; BC
Lonchocarpus domingensis	1; G
Lonchocarpus pentaphyllus	1; BC
Lonchocarpus spiciflorus	1; M
Lonchocarpus velutinus	1; BC
Machaerium arboreum	1; BC
Machaerium floribundum	1; BC
Machaerium hirtum	1; BE
Machaerium kegelii	1; BC
Machaerium lunatum	1; SM
Machaerium microphyllum	1; BC
Machaerium milleflorum	1; BC
Machaerium riparium	1; BC
Machaerium seemanni	1; BC
Mimosa ceratonia	1; SD,SM
Mimosa pigra	1; BC
Mimosa pudica	1; SM
Mucuna mutisiana	1; BC
Myroxylon balsamum	1; BC
Neorudolphia volubilis	1; BI
Ormosia coccinea	1; BC
Ormosia krugii	1; BI
Ormosia macrocalyx	1; BC
Ormosia panamensis	1; BC
Parkia multijuga	1; M
Parkia nitida	1; M
Parkia velutina	1; M
Peltogyne purpurea	1; BC
Pictetia aculeata	1; G,SD,SM
Piptadenia suaveolens	1; M

Species	Margin; sample(s)
Piscidia carthagenensis	1; G,SD,SM
Pithecellobium angustifolium	1; BE
Pithecellobium barbourianum	1; BC
Pithecellobium basijugum	1; M
Pithecellobium corymbosum	1; M
Pithecellobium dinizii	1; BC
Pithecellobium hymenaefolium	1; BC
Pithecellobium latifolium	1; BE,M
Pithecellobium macradenium	1; BC
Pithecellobium rufescens	1; BC
Pithecellobium unguis-cati	1; G,SD,SM
Platymiscium sp.	1; BE
Platypodium elegans	1; BC
Prioria copaifera	1; BC
Prosopis juliflora	1; G
Pterocarpus officinalis	1; BC,BI
Pterocarpus rohrii	1; BC
Pterocarpus rohrii aff.	1; M
Rhyncosia pyramidalis	1; BC
Rhyncosia reticulata	1; SD
Robinia pseudoacacia	1; A,Y
Sabinea florida	1; SD,SM
Sesbania sericea	1; SM
Schizolobium parahybum	1; BC,M
Sclerolobium bracteosum	1; M
Senna silvestris	1; M
Stylosanthes hamata	1; SD
Swartzia 2	1; BE
Swartzia 12799	1; M
Swartzia jojori	1; BE
Swartzia panamensis	1; BC
Swartzia simplex	1; BC
Tachigali polyphylla	1; M
Tachigali versicolor	1; BC
Teramnus labialis	1; SM
Vatairea erythrocarpa	1; BC
Vigna luteola	1; SM
12862	1; M
FAGACEAE	
Castanea dentata	0; A,Y
Fagus grandifolia	0; A,Y

Species	Margin; sample(s)
Quercus alba	1; A,Y
Quercus coccinea	0; Y
Quercus ilicifolia	0; Y
Quercus prinoides	0; Y
Quercus prinus	0; A,Y
Quercus rubra	0; A,Y
Quercus velutina	0.5; Y
FLACOURTIACEAE	
Banara guianensis	0; BC,M
Casearia aculeata	0; BC
Casearia arborea	0; BC,BI,M
Casearia arguta	0; BC
Casearia corymbosa	0; BC
Casearia decandra	0; SD,SM
Casearia guianensis	0; BC,BI,SD,SM
Casearia obovalis cf	1; M
Casearia sylvestris	0; BC,BE,BI,SM
Hasseltia floribunda	0; BC
Homalium racemosum	0; BI,G
Laetia corymbulosa	0; M
Laetia procera	0; BC,BI,M
Laetia thamnia	0; BC
Lindackeria laurina	1; BC
Lindackeria paludosa	1; M
Lunania parviflora	1; M
Mayna parvifolia	1; M
Prockia crucis	0; SD
Samyda dodecandra	0; G,SD,SM
Tetrathylacium johansenii	0.5; BC
Tetrathylacium macrophyllum	0; M
Xylosma buxifolium	0.5; SD,G
Xylosma chloranthum	0; BC
Xylosma oligandrum	0; BC
Zuelania guidonia	0; BC
GESNERIACEAE	
Codonanthe crassifolia	0; BC
Columnea billbergiana	0; BC
Drymonia serrulata	0; BC
GNETACEAE	
Gnetum leyboldii	1; BC
GROSSULARIACEAE	
Ribes americanum	0; Y
Ribes cynosbasti	0; A
Ribes glandulosum	0; A

Species	Margin; sample(s)
Ribes hirtellum	0; Y
Ribes rotundifolium	0; A
Ribes triste	0; A
HAMAMELIDACEAE	
Hamamelis virginiana	0; A,Y
HIPPOCRATEACEAE	
Anthodon panamense	1; BC
Cheiloclinium cognatum	1; M
Hippocratea volubilis	0.5; BC
Hylenaea praecelsa	1; BC
Prionostemma aspera	1; BC
Salacia 1	1; BE
Salacia 2	1; BE
Salacia macrantha	1; M
Tontelea richardii	1; BC
HOUMIRIACEAE	
Vantanea occidentalis	1; BC
ICACINACEAE	
Calatola venezuelana	0; M
JUGLANDACEAE	
Carya cordiformis	0; A,Y
Carya glabra	0; Y
Carya laciniosa	0; Y
Carya ovalis	0; Y
Carya ovata	0; A,Y
Carya tomentosa	0; Y
LACISTEMACEAE	
Lacistema aggregatum	0.5; BC,BE,M
Lozania pittieri	0.5; BC
LAURACEAE	
Aniba 1877	1; M
Aniba 12054	1; M
Aniba bracteata	1; BI
Beilschmiedia pendula	1; BC,BI
Cinnamomum elongatum	1; SM
Endlicheria 1993	1; M
Endlicheria tessmannii	1; M
Endlicheria x	1; M
Licaria salicifolia	1; G,SD,SM
Licaria triandra	1; BI,SM
Lindera benzoin	1; Y
Ocotea caucana	1; BE
Ocotea cernua	1; BC
Ocotea cissiflora	1; BC
Ocotea coriacea	1; SD,SM
Ocotea cuspidata	1; M
Ocotea floribunda	1; SM
Ocotea globosa	1; BC,BI
Ocotea leucoxylon	1; BI,SM
Ocotea longifolia	1; BE.M
Ocotea membranacea	1; BI
Ocotea moschata	1; BI
Ocotea oblonga	1; BC
Ocotea portoricensis	1; BI
Ocotea pulverulenta	1; M
Ocotea purpurescens	1; BC
Ocotea pyramidata	1; BC
Ocotea savanarrum	1; BC
Ocotea sintensii	1; BI
Ocotea skutchii	1; BC
Ocotea sp.	1; BE
Ocotea turbacensis	1; BE
Persea coerulea	1; BE
Phoebe mexicana	1; BC
Pleurothyrium krukovii	1; M
Sassafras albidum	1; A,Y
sp.	1; M
LECYTHIDACEAE	
Couratari guianensis	1; M
Couratari panamensis	0.5; BC
Eschweilera coriacea	1; M
Grias fendleri	1; BC
Gustavia fosteri	0; BC
Gustavia hexapetala	0; M
Gustavia superba	0; BC
LOGANIACEAE	
Strychnos brachistantha	1; BC
Strychnos darienensis	1; BC
Strychnos panamensis	1; BC
Strychnos toxifera	1; BC
LYTHRACEAE	
Adenaria floribunda	1; BC
Ginoria rohrii	1; SD,SM
Lafoënsia punicifolia	1; BC
MAGNOLIACEAE	
Liriodendron tulipifera	1; A,Y
Magnolia acuminata	1; A,Y
Magnolia splendens	1; BI
MALPIGHIACEAE	
Banisteriopsis cornifolia	1; BC
Bunchosia cornifolia	1; BC
Bunchosia glandulosa	1; G; SD,SM

Species	Margin; sample(s)
Byrsonima 12596	1; M
Byrsonima arthropoda	1; M
Byrsonima coriacea	1; SD,SM
Byrsonima crassifolia	1; BC
Byrsonima spicata	1; BC,BE,BI
Heteropterys laurifolia	1; BC,BE,BI
Heteropterys purpurea	1; SD,SM
Hiraea faginea	1; BC
Hiraea grandifolia	1; BC
Hiraea quapara	1; BC
Hiraea reclinata	1; BC
Malpighia romeroana	1; BC
Mascagnia hippocrateoides	1; BC
Mascagnia nervosa	1; BC
Spachea membranacea	1; BC
Stigmaphyllon ellipticum	1; BC
Stigmaphyllon hypargyreum	0.5; BC
Stigmaphyllon lindenianum	0.5; BC
Stigmaphyllon periplocifolium	1; SD,SM
Stigmaphyllon puberum	1; BC
Stigmaphyllon tomentosum	1; SM
Tetrapteris discolor	1; BC
Tetrapteris macrocarpa	1; BC
Tetrapteris seemannii	1; BC
MALVACEAE	
Abutilon umbellatum	0; SD
Hampea appendiculata	1; BC
Hibiscus bifurcatus	0; BC
Hibiscus sororius	0; BC
Malvastrum americana	0; SD
Malvastrum corchorifolium	0; SD
Malvastrum coromandelianum	0; SD
Pavonia dasypetala	0; BC
Pavonia fruticosa	0; BI
Pavonia paniculata	0; BC
Pavonia spinifex	0; SD,SM
Sida acuminata	0; SD,SM
Sida acuta	0; SD,SM
Sida cordifolia	0; SD,SM
Sida glomerata	0; SD,SM
Sida rhombifolia	0; BI

Species	Margin; sample(s)
Thespesia grandiflora	1; BI
Thespesia populnea	1; SD,SM
Urena lobata	0; BI,SM
MARCGRAVIACEAE	
Marcgravia nepenthoides	1; BC
Marcgravia rectiflora	1; BI
Marcgravia sintensii	1; BI
Souroubea sympetala	1; BC
MELASTOMATACEAE	
Adelobotrys adscendens	0.5; BC
Bellucia grossularioides	1; BC
Calycogonium squamulosum	1; BI
Clidemia capitellata	0; BC
Clidemia collina	1; BC
Clidemia dentata	0.5; BC
Clidemia octona	0; BC
Clidemia purpureo-violacea	0; BC
Clidemia septuplinervia	1; BC
Conostegia bracteata	0; BC
Conostegia cinnamomea	1; BC
Conostegia speciosa	0; BC
Conostegia xalapensis	0; BC
Henriettea fascicularis	1; BI
Henriettea succosa	1; BC
Leandra dichotoma	0; BC
Miconia affinis	1; BC
Miconia argentea	0.5; BC
Miconia argyrophylla	1; M
Miconia borealis	1; BC
Miconia elata	0; BC
Miconia hondurensis	1; BC
Miconia impetiolaris	0.5; BC
Miconia lacera	0.5; BC
Miconia laevigata	1; BI,SM
Miconia lateriflora	0; BC
Miconia lonchophylla	1; BC
Miconia nervosa	1; BC
Miconia prasina	0.5; BC,BI
Miconia racemosa	0; BI
Miconia rufostellulata	0.5; BC
Miconia serrulata	0; BC,BI
Miconia tetrandra	1; BI
Mouriri myrtilloides	1; BC
Ossaea quinquenervia	0; BC
Tetrazygia angustifolia	1; SD,SM

Species	Margin; sample(s)
Tetrazygia elaeagnoides	1; SD,SM
Tetrazygia urbanii	1; BI
Topobea praecox	1; BC
MELIACEAE	
Cabralea cangerana	1; M
Cedrela fissilis	1; M
Cedrela odorata	1; BC
Guarea glabra	1; BC,BI
Guarea guidonia	1; BE,BI
Guarea kunthiana	1; M
Guarea macrophylla	1; M
Guarea multiflora	1; BC
Trichilia cipo	1; BC
Trichilia elegans	1; M
Trichilia hirta	1; BC,G
Trichilia maynasiana	1; M
Trichilia montana	1; BC
Trichilia pachypoda cf	1; M
Trichilia pallida	1; BE,BI,M
Trichilia pleeana	1; BE,M
Trichilia poeppigii	1; M
Trichilia rubra	1; M
Trichilia solitudinis	1; M
Trichilia sp.	1; M
Trichilia triacantha	1; G
Trichilia verrucosa	1; BC
MENISPERMACEAE	
Abuta grandifolia	1; M
Abuta panamensis	1; BC
Abuta racemosa	0.5; BC
Chondrodendron tomentosum	1; BC
Cissampelos pareira	1; BC,BI,SM,SD
Cissampelos tropaeolifolia	1; BC
Hyperbaena domingensis	1; SM
Odontocarya tamoides	1; BC
Odontocarya truncata	1; BC
MONIMIACEAE	
Siparuna decipiens	1; M
Siparuna guianensis	1; BC
Siparuna pauciflora	1; BC
MORACEAE	
Batocarpus amazonicus	0; M
Brosimum alicastrum	1; BC,M
Brosimum guianense	1; BE,M

Species	Margin; sample(s)
Brosimum lactescens	1; BE,M
Castilla elastica	0; BC
Castilla ulei	0; M
Cecropia engleriana	1; M
Cecropia insignis	1; BC
Cecropia latiloba	1; M
Cecropia longipes	1; BC
Cecropia obtusifolia	1; BC
Cecropia peltata	1; BC,BI,SM
Cecropia sciadophylla	1; M
Cecropia sp.	1; M
Cecropia sp.	1; BE
Cecropia tessmannii	1; M
Clarisia biflora	1; BE,M
Clarisia racemosa	1; M
Coussapoa magnifolia	1; BC
Coussapoa panamensis	1; BC
Ficus 5	1; BE
Ficus bullenei	1; BC
Ficus casapiensis #2	1; M
Ficus citrifolia(laevigata)	1; G,BC,BI,SD,SM
Ficus colubrinae	1; BC
Ficus costaricana	1; BC
Ficus dugandii	1; BC
Ficus insipida	1; BC,BE,M
FIcus killipii	1; BE,M
Ficus mathewsii	1; M
Ficus maxima	1; BC,BE,M
Ficus nymphiifolia	1; BC
Ficus obtusifolia	1; BC
Ficus paraensis	1; BC,M
Ficus perez-arbelaezii	1; M
Ficus perforata	1; BC
Ficus pertusa	1; BC
Ficus popenoei	1; BC
Ficus sintensii	1; G
Ficus sp.	1; M
Ficus tonduzii	1; BC
Ficus trigona	1; BE,M
Ficus trigonata	1; BC,SM
Ficus yoponensis	1; BC
Maclura tinctoria	0; BE
Maquira calophylla	1; M
Maquira costaricana	1; BC
Olmedia aspera	0; BC

Species	Margin; sample(s)
Perebea guianensis	0; M
Perebea xanthochyma	1; BC
Poulsenia armata	1; BC,M
Pourouma cecropiifolia	1; M
Pourouma guianensis	1; BC,M
Pourouma minor	1; M
Pourouma mollis	1; M
Pseudolmedia laevigata	1; M
Pseudolmedia laevis	1; BE,M
Pseudolmedia murure	1; M
Pseudolmedia spuria	1; BC
Sorocea affinis	1; BC
Sorocea pileata	0; M
Sorocea saxicola	0.5; BE
Trophis racemosa	0.5; BC
MYOPORACEAE	
Bontia daphnoides	1; SM
MYRICACEAE	
Comptonia peregrina	1; A,Y
Myrica pennsylvanica	0; Y
MYRICACEAE	
Compsoneura sprucei	1; BC
Iryanthera juruensis	1; M
Otoba parvifolia	1; M
Virola calophylla	1; BE,M
Virola duckei	1; M
Virola flexuosa	1; M
Virola mollissima	1; M
Virola sebifera	1; BC,BE
Virola surinamensis	1; BC
MYRSINACEAE	
Ardisia fendleri	1; BC
Ardisia obovata	1; SD,SM
Ardisia pellucida	0; BC
Myrsine umbellata	1; BE
Parathesis crenulata	0; BI
Parathesis microcalyx	1; BC
Stylogyne standleyi	1; BC
Wallenia pendula	1; BI
MYRTACEAE	
Calycolpus warscewiczianus	1; BC
Calyptranthes densiflora	1; M
Calyptranthes pallens	1; BI,G
Calyptranthes thomasiana	1; SM
Eugenia axillaris	1; G,SD,SM
Eugenia biflora	1; G,SD,SM
Eugenia boqueronensis	1; G
Eugenia coloradensis	1; BC
Eugenia confusa	1; SM
Eugenia cordata	1; SD,SM
Eugenia eggersii	1; BI
Eugenia foetida	1; G
Eugenia galalonensis	1; BC
Eugenia ligustrina	1; G,SD,SM
Eugenia monticola	1; G,SD,SM
Eugenia muricata	1; M
Eugenia myrobalana	1; M
Eugenia nesiotica	1; BC
Eugenia oerstedeana	1; BC
Eugenia principium	1; BC
Eugenia procera	1; SD,SM
Eugenia pseudopsidium	1; SD,SM
Eugenia rhombea	1; G,SD,SM
Eugenia sessiliflora	1; SD
Eugenia sp.	1; BE
Eugenia stahlii	1; BI
Eugenia venezuelensis	1; BC
Eugenia xerophytica	1; G
Myrcia citrifolia	1; SD,SM
Myrcia deflexa	1; BI
Myrcia fosteri	1; BC
Myrcia gatunensis	1; BC
Myrcia leptoclada	1; BI
Myrcia splendens	1; BI,M
Myrcia sylvatica	1; M
Myrcianthes fragrans	1; G,SD,SM
Myrciaria floribunda	1; G,SD,SM
Pimenta racemosa	1; SD.SM
Psidium acutangulum	1; M
Psidium amplexicaule	1; SD,SM
Psidium anglohondurense	1; BC
Psidium friedrichsthalianum	1; BC
Syzygium jambos	1; BI
sp.	1; M
NYCTAGINACEAE	
Guapira 11340	1; M
Guapira 11345	1; M
Guapira fragrans	1; SD,SM
Guapira obtusata	1; G
Guapira sp.	1; BE

Species	Margin; sample(s)
Guapira standleyanum	1; BC
Neea 1851	1; M
Neea 5451	1; M
Neea 11941	1; M
Neea amplifolia	1; BC
Neea buxifolia	1; SD
Neea comun	1; M
Neea sp.	1; M
Pisonia aculeata	1; BC,SM
Pisonia albida	1; G
Pisonia subcordata	1; SD,SM
NYSSACEAE	
Nyssa sylvatica	1; Y
OCHNACEAE	
Cespedesia macrophylla	0; BC
Ouratea lucens	0; BC
Ouratia littoralis	0.5; SM
OLACACEAE	
Heisteria acuminata	1; M
Heisteria concinna	1; BC
Heisteria costaricensis	1; BC
Heisteria longipes	1; BC
Heisteria nitida	1; BE
Heisteria ovata	1; M
Minquartia guianensis	1; M
Schoepfia obovata	1; G
Schoepfia schreberi	1; SD,SM
Ximenia americana	1; G,SD,SM
OLEACEAE	
Chionanthus domingensis	1; BI
Forestiera segregata	1; G
Fraxinus americana	0.5; A,Y
Linociera caribaea	1; SD,SM
Linociera holdridgii	1; G
ONAGRACEAE	
Ludwigia octovalvis	1; SM
PASSIFLORACEAE	
Passiflora laurifolia	1; SM
Passiflora multiflora	1; SD,SM
Passiflora vitifolia	0; BC
PHYTOLACCACEAE	
Gallesia integrifolia	1; BE,M
Phytolacca rivinoides	1; BI
Trichostigma octandrum	1; BI,SD,SM
PIPERACEAE	
Lepianthes peltata	1; BI

Species	Margin; sample(s)
Piper aduncum	1; BI
Piper aequale	1; BC
Piper arboreum	1; BC
Piper arieianum	1; BC
Piper aristolochiifolium	1; BC
Piper auritum	1; BC
Piper carilloanum	1; BC
Piper cordulatum	1; BC
Piper culebranum	1; BC
Piper darienense	1; BC
Piper dilatatum	1; BC
Piper glabrescens	1; BI
Piper grande	1; BC
Piper hispidum	1; BC,BI
Piper imperiale	1; BC
Piper jacquemontianum	1; BI
Piper marginatum	1; BC
Piper peracuminatum	1; BC
Piper perlasense	1; BC
Piper pseudo-garagaranum	1; BC
Piper pubistipulum	1; BC
Piper reticulatum	1; BC
Piper tuberculatum	1; BE
Piper villiramulum	1; BC
Piper viridicaule	1; BC
Piper amalago	1; SM
PLATANACEAE	
Platanus occidentalis	0; Y
PLUMBAGINACEAE	
Plumbago scandens	1; SD
POLYGALACEAE	
Polygala cowelii	1; G
Polygala penaea	1; G
Securidaca diversifolia	1; BC
Securidaca tenuifolia	1; BC
Securidaca virgata	1; BI
POLYGONACEAE	
Antigonon leptopus	1; SM
Coccoloba acapulcensis	1; BC
Coccoloba acuminata	1; BC
Coccoloba cordata	1; BE
Coccoloba coronata	1; BC
Coccoloba densifrons	1; M
Coccoloba diversifolia	1; G
Coccoloba krugii	1; G

Species	Margin; sample(s)
Coccoloba manzanillensis	1; BC
Coccoloba microstachya	1; G,SD
Coccoloba mollis	1; M
Coccoloba parimensis	1; BC
Coccoloba swartzii	1; SD
Coccoloba uvifera	1; SD,SM
Coccoloba venosa	1; G,SM
Coccoloba williamsii	1; M
Triplaris americana	1; BE,M
Triplaris cumingiana	1; BC
PROTEACEAE	
Roupala montana	1; BC
QUIINACEAE	
Quiina macrophylla	1; M
RANUNCULACEAE	
Clematis virginiana	0; A
RHAMNACEAE	
Ceanothus americanus	0; Y
Colubrina arborescens	1; G,SD,SM
Colubrina elliptica	1; G,SD
Colubrina glandulosa	1; BC
Gouania lupuloides	1; BC,SD,SM
Krugiodendron ferreum	1; G,SD,SM
Reynosia guama	1; G,SD,SM
Reynosia uncinata	1; G
Rhamnidium elaeocarpum	1; BE
Sarcomphalus reticulatus	0; G
Zizyphus cinnamomum	1; M
RHIZOPHORACEAE	
Cassipourea elliptica	0; BC
Cassipourea guianensis	1; BI
ROSACEAE	
Amelanchier arborea	0; A,Y
Amelanchier laevis	0; A,Y
Aronia arbutifolia	0; Y
Aronia melanocarpa	0; Y
Aronia prunifolia	0; Y
Crataegus coccinea	0; Y
Crataegus crus-galli	0; Y
Crataegus pruinosa	0; Y
Crataegus rotundifolia	0; Y
Physocarpus opulifolius	0; Y
Prunus americana	0; A,Y
Prunus pennsylvanica	0; A,Y
Prunus serotina	0; A,Y

Species	Margin; sample(s)
Prunus virginiana	0; A,Y
Rosa carolina	0; Y
Rosa palustris	0; Y
Rubus allegheniensis	0; A,Y
Rubus canadensis	0; A
Rubus enslenii	0; Y
Rubus flagellaris	0; Y
Rubus hispidus	0; A,Y
Rubus idaeus	0; A,Y
Rubus occidentalis	0; A,Y
Rubus odoratus	0; A,Y
Rubus pennsylvanicus	0; A,Y
Rubus recurvicaulis	0; Y
Rubus "sp. 3"	0; Y
Sorbus americana	0; A,Y
Spiraea alba	0; Y
Spiraea latifolia	0; Y
RUBIACEAE	
Alibertia edulis	1; BC
Alseis blackiana	1; BC
Alseis blackiana cf	1; M
Amaioua corymbosa	1; BC
Antirhea acutata	1; G
Antirhea lucida	1; G
Antirhea trichantha	1; BC
Bertiera guianensis	1; BC
Calycophyllum acreanum	1; M
Calycophyllum candidissimum	1; BC
Calycophyllum spruceanum	1; BE.M
Capirona decorticans	1; M
Cephaelis discolor	1; BC
Cephaelis ipecacuanha	1; BC
Cephaelis tomentosa	1; BC
Cephalanthus occidentalis	1; A,Y
Chimarrhis 1818	1; M
Chimarrhis parviflora	1; BC
Chiococca alba	1; BC,SD,SM
Chione venosa	1; SM
Chomelia psilocarpa	1; BC
Chomelia spinosa	1; BE
Cosmibuena skinneri	1; BC
Coussarea curvigemmia	1; BC
Coutarea hexandra	1; BC
Erithalis fruticosa	1; G,SD

Species	Margin; sample(s)
Exostema caribaeum	1; G,SD
Faramea luteovirens	1; BC
Faramea occidentalis	1; BC,BI,M,SD,SM
Faramea sp.	1; BE
Genipa americana	1; BC,BE,M,SM
Gonzalagunia spicata	1; BI,SM
Guettarda elliptica	1; G
Guettarda foliacea	1; BC
Guettarda krugii	1; G
Guettarda odorata	1; SD,SM
Guettarda scabra	1; SD,SM
Guettarda viburnoides	1; BE
Hamelia axillaris	1; BC
Hamelia patens	1; BC,BI
Hemidiodia ocimifolia	1; BI
Hoffmannia woodsonii	1; BC
Isertia haenkeana	1; BC
Ixora ferrea	1; BI,SM
Ixora peruviana	1; M
Machaonia portoricensis	1; G
Macrocnemum glabrescens	1; BC
Macrocnemum roseum	1; M
Palicourea crocea	1; BI
Palicourea domingensis	1; SM
Palicourea guianensis	1; BC
Palicourea riparia	1; SM
Pentagonia macrophylla	1; BC
Pogonopus speciosus	1; BC
Posoqueria latifolia	1; BC
Psychotria acuminata	1; BC
Psychotria berteriana	1; BI
Psychotria brachiata	1; BC,BI
Psychotria brachybotrya	1; BC
Psychotria brownei	1; SD,SM
Psychotria capitata	1; BC
Psychotria carthagenensis	1; BC
Psychotria chagrensis	1; BC
Psychotria deflexa	1; BC
Psychotria emetica	1; BC
Psychotria furcata	1; BC
Psychotria granadensis	1; BC
Psychotria grandis	1; BC

Species	Margin; sample(s)
Psychotria horizontalis	1; BC
Psychotria limonensis	1; BC
Psychotria maleolens	1; BI
Psychotria marginata	1; BC
Psychotria micrantha	1; BC
Psychotria microdon	1; SD,SM
Psychotria nervosa	1; SD,SM
Psychotria pittieri	1; BC
Psychotria psychotriaefolia	1; BC
Psychotria pubescens	1; BC
Psychotria racemosa	1; BC
Psychotria uliginosa	1; BC
Randia aculeata	1; SD,SM
Randia armata	1; BC,BE
Randia formosa	1; BC
Rondeletia inermis	1; G
Rondeletia pilosa	1; SD,SM
Rondeletia portoricensis	1; BI
Sabicea hirsuta	1; BI
Sabicea villosa	1; BC
Tocoyena pittieri	1; BC
Uncaria tomentosa	1; BC
Warscewiczia coccinea	1; BC
RUTACEAE	
Amyris elemifera	1; G
Galipea trifoliata	1; M
Metrodorea flavida	1; M
Neoraputia paraensis	1; M
Pilocarpus racemosus	1; SM
Ravenia urbanii	1; BI
Zanthoxylum americanum	0; Y
Zanthoxylum belizense	1; BC
Zanthoxylum flavum	0.5; G
Zanthoxylum martinicensis	0; G,BI,SD,SM
Zanthoxylum monophyllum	1; G,SD,SM
Zanthoxylum panamense	0.5; BC
Zanthoxylum procerum	0; BC
Zanthoxylum setulosum	0.5; BC
Zanthoxylum sp.	1; BE
Zanthoxylum spinifex	1; G
Zanthoxylum thomasianum	0.5; SD
SABIACEAE	

Species	Margin; sample(s)
Meliosma herbertii	1; BI
SALICACEAE	
Populus grandidentata	0; A,Y
Populus tremuloides	0; A,Y
Salix bebbiana	0; A
Salix discolor	0; A
Salix eriocephala	0; A,Y
Salix exigua	0; A
Salix humilis	1; A,Y
Salix lucida	0; A
Salix nigra	0; A,Y
Salix sericea	0; A,Y
Salix "sp. 2"	0; Y
SAPINDACEAE	
Allophylus divaricatus	0; M
Allophylus psilospermus	0; BC
Allophylus racemosus	0; G,SD,SM
Allophylus scrobiculatus	0; M
Cupania americana	0; BI
Cupania cinerea	0; BC,BE
Cupania latifolia	0; BC
Cupania rufescens	0; BC
Cupania sylvatica	1; BC
Cupania triquetra	0.5; SD,SM
Exothea paniculata	1; G,SD,SM
Hypelate trifoliata	1; G
Matayba 12764	0; M
Matayba domingensis	1; BI
Paullinia baileyi	0; BC
Paullinia bracteosa	0; BC
Paullinia fibrigera	0.5; BC
Paullinia glomerulosa	0.5; BC
Paullinia pinnata	0; BC,BI
Paullinia pterocarpa	0; BC
Paullinia rugosa	0; BC
Paullinia turbacensis	0; BC
Pseudima frutescens	1; M
Serjania atrolineata	0; BC
Serjania circumvallata	0; BC
Serjania cornigera	0; BC
Serjania decapleuria	0.5; BC
Serjania mexicana	0; BC
Serjania paucidentata	0; BC
Serjania pluvialiflorens	0; BC
Serjania rhombea	0; BC
Serjania trachygona	0; BC

Species	Margin; sample(s)
Talisia hexaphylla	1; BE
Talisia nervosa	1; BC
Talisia princeps	1; BC
Thinouia myriantha	0; BC
Thouinia portoricensis	0; G
Toulicia reticulata	1; BE
SAPOTACEAE	
Chrysophyllum argenteum	1; BI,M
Chrysophyllum cainito	1; BI
Chrysophyllum eggersii	1; SM
Chrysophyllum pauciflorum	1; SD,SM
Chrysophyllum venezuelanense	1; M
Cynodendron panamense	1; BC
Dipholis obovata	1; G,SD,SM
Dipholis salicifolia	1; G,SD,SM
Ecclinusa guyanensis	1; M
Manilkara bidentata	1; BI,SM
Manilkara inundata	1; M
Micropholis chrysophylloides	1; BI
Micropholis egensis	1; M
Micropholis garciniaefolia	1; BI
Micropholis guyanensis	1; M
Micropholis melinoniana	1; M
Pouteria 1999	1; M
Pouteria caimito	1; M
Pouteria durlandii	1; M
Pouteria ephedrantha	1; M
Pouteria fossicola	1; BC
Pouteria macrophylla	1; BE,M
Pouteria multiflora	1; BI,SM
Pouteria pariry cf	1; M
Pouteria procera	1; M
Pouteria sapota	1; BC
Pouteria sp.	1; M
Pouteria stipitata	1; BC
Pouteria tarapotensis	1; M
Pouteria torta	1; M
Pouteria unilocularis	1; BC
Sarcaulus brasiliensis	1; M
6523	1; M
SAXIFRAGACEAE	
Hydrangea arborescens	0; Y

Species	Margin; sample(s)
Hydrangea peruviana	1; BC
SCROPHULARIACEAE	
Capraria biflora	0; SD,SM
SIMAROUBACEAE	
Picramnia 12766	1; M
Picramnia latifolia	1; BC
Picramnia pentandra	1; G
Picrasma excelsa	1; SM
Simaba gracile	1; BE
Simarouba amara	1; BC
Suriana maritima	1; G
SMILACACEAE	
Smilax lanceolata	1; BC
Smilax rotundifolia	1; Y
SOLANACEAE	
Brunfelsia americana	1; SM
Capsicum frutescens	1; SM
Cestrum latifolium	1; BC
Cestrum laurifolium	1; SD,SM
Cestrum macrophyllum	1; BI
Cestrum megalophyllum	1; BC
Cestrum nocturnum	1; BC
Cestrum racemosum	1; BC
Cyphomandra hartwegii	1; BC
Datura stramonium	0; SM
Lycianthes maxonii	1; BC
Lycianthes synanthera	1; BC
Markea ulei	1; BC
Solanum antillarum	1; BC
Solanum arboreum	1; BC
Solanum argenteum	1; BC
Solanum asperum	1; BC
Solanum conocarpum	1; SM
Solanum erianthum	1; G,SM
Solanum grandiflorum	0; BE
Solanum hayesii	1; BC
Solanum jamaicense	1; BC
Solanum lancifolium	1; BC,SD,SM
Solanum ochraceo-ferrugineum	1; BC
Solanum persicaefolium	1; SD
Solanum polygamum	1; SD,SM
Solanum racemosum	1; SM
Solanum rugosum	1; BC
Solanum subirerme	1; BC
Solanum torvum	1; BI,SM
Solanum umbellatum	1; BC
Witheringia solanacea	1; BC
STAPHYLEACEAE	
Huertea glandulosa	0; M
Staphylea trifolia	0; Y
Turpinia occidentalis	0; BC,BI,M
STERCULIACEAE	
Byttneria aculeata	0.5; BC
Guazuma crinita	0; M
Guazuma ulmifolia	0; BC,BE,G,M,SD,SM
Helicteres jamaicensis	0; G,SD,SM
Herrania purpurea	0.5; BC
Melochia lupulina	0; BC
Melochia nodiflora	0; SD,SM
Melochia tomentosa	0; G,SD
Sterculia apetala	1; BC,BE,M
Theobroma cacao	1; M
Theobroma speciosum	1; M
Waltheria glomerata	0; BC
Waltheria indica	0; SD,SM
SYMPLOCACEAE	
Symplocos martinicensis	0; SM
THEACEAE	
Laplacea portoricensis	0; BI
Ternstroemia peduncularis	1; SM
Ternstroemia tepezapote	1; BC
THEOPHRASTACEAE	
Jacquinia arborea	1; G,SD
Jacquinia berterii	1; G,SD
THYMELAEACEAE	
Daphnopsis americana	1; G,SD,SM
Dirca palustris	1; A,Y
TILIACEAE	
Apeiba "hybrid"	0; M
Apeiba membranacea	1; BC,M
Apeiba tibourbou	0; BC,BE
Heliocarpus popayensis	0; BC
Luehea cymulosa	0; BE,M
Luehea seemannii	0; BC
Luehea speciosa	0; BC
Luehea paniculata	0; BE
Tilia americana	0; A,Y
Trichospermum mexicanum	0; BC
Triumfetta lappula	0; BC,SM

Species	Margin; sample(s)
Triumfetta semitriloba	0; SM
TRIGONIACEAE	
Trigonia floribunda	1; BC
TURNERACEAE	
Turnera panamensis	0; BC
Turnera ulmifolia	0; SM
ULMACEAE	
Ampelocera edentula	1; M
Ampelocera ruizii	0; BE
Celtis iguanaea	0; BC,SM
Celtis occidentalis	0; Y
Celtis schippii	1; BC,BE,M
Celtis trinervia	0; G,SD,SM
Trema micranthum	0; BC,BI,M,SD,SM
Ulmus americana	0; A,Y
Ulmus rubra	0; A
URTICACEAE	
Myriocarpa yzabalensis	0; BC
Pouzolzia obliqua	1; BC
Urera baccifera	0; BI
Urera caracasana	0; M
Urera eggersii	0.5; BC
VERBENACEAE	
Aegiphila cephalophora	1; BC
Aegiphila elata	1; BC
Aegiphila panamensis	1; BC
Citharexylum fruticosum	0.5; G,SD,SM
Clerodendrum aculeatum	1; G,SM
Duranta repens	1; G
Lantana involucrata	0; SD,SM
Lantana urticifolia	0; SD
Petrea aspera	1; BC
Vitex cooperii	1; BC
Vitex cymosa	1; M
Vitex divaricata	1; BI,SM
VIOLACEAE	
Hybanthus prunifolius	0; BC
Leonia glycycarpa	1; M
Rinorea apiculata	0; M
Rinorea guianensis	0; M
Rinorea lindeniana	0; M
Rinorea squamata	0; BC
Rinorea sylvatica	0; BC
Rinorea viridifolia	0; M
Rinoreocarpus 12708	0; M

Species	Margin; sample(s)
Rinoreocarpus 12724	0; M
Rinoreocarpus ulei	0; M
VITACEAE	
Cissus erosa	0; BC,BI
Cissus microcarpa	0; BC
Cissus pseudosicyoides	0; BC
Cissus rhombifolia	0; BC
Cissus verticillata (sicyoides)	0; BC,BI
Parthenocissus quinquefolia	0; Y
Vitis aestivalis	0; Y
Vitis riparia	0; Y
Vitis tiliifolia	0; BC,SM
Vitis labrusca	0; Y
Vitis vulpina	0; Y
VOCHYSIACEAE	
Erisma uncinatum	1; M
Qualea grandiflora	1; M
Vochysia ferruginea	1; BC
Vochysia mapirensis	1; BE
ZYGOPHYLLACEAE	
Guaiacum officinale	1; G
Guaiacum sanctum	1; G

CHAPTER THREE

USING FOSSIL LEAVES AS PALEOPRECIPITATION INDICATORS: AN EOCENE EXAMPLE

This chapter is written in the style of the journal *Geology*, where it has been published (v. 26, p. 203-206, 1998). Coauthors S. L. Wing, D. R. Greenwood, and C. L. Greenwood contributed the Eocene leaf-area data.

Using fossil leaves as paleoprecipitation indicators: An Eocene example

Peter Wilf

Scott L. Wing

Department of Paleobiology, MRC 121, National Museum of Natural History,
Smithsonian Institution, Washington, D. C. 20560

David R. Greenwood

Department of Biological and Food Sciences, Victoria University of
Technology, St. Albans Campus, PO Box 14428, MCMC, Melbourne, VIC 8001,
Australia

Cathy L. Greenwood

Department of Geography and Environmental Science, Monash
University, Wellington Road, Clayton, VIC 3168, Australia

ABSTRACT

Estimates of past precipitation are of broad interest for many areas of inquiry, including reconstructions of past environments and topography, climate modeling, and ocean circulation studies. The shapes and sizes of living leaves are highly sensitive to moisture conditions, and assemblages of fossil leaves of flowering plants have great potential as paleoprecipitation indicators. Most quantitative estimates of paleoprecipitation have been based on a multivariate data set of morphological leaf characters measured from samples of living vegetation tied to climate stations. However, when tested on extant forests, this

method has consistently overestimated precipitation. We present a simpler approach that uses only the mean leaf area of a vegetation sample as a predictor variable but incorporates a broad range of annual precipitation and geographic coverage into the predictor set. The significant relationship that results, in addition to having value for paleoclimatic reconstruction, refines understanding of the long-observed positive relationship between leaf area and precipitation. Seven precipitation estimates for the Eocene of the Western U. S. are revised as lower than previously published but remain far wetter than the same areas today. Abundant moisture may have been an important factor in maintaining warm, frost-free conditions in the Eocene because of the major role of water vapor in retaining and transporting atmospheric heat.

INTRODUCTION

Fossil leaves are a rich source of information about past rainfall because the morphologies of living leaves, and leaf size in particular, are greatly influenced by available moisture (Raunkiaer, 1934; Richards, 1996). Because leaves transpire water into the atmosphere and have a high ratio of surface area to volume, plants in drier climates tend to have smaller leaves because they can not afford the elevated water loss required to maintain large leaves (Givnish, 1984). Available water, which is controlled by many factors including precipitation, evapotranspiration, temperature, seasonality, and soil conditions, appears to be the primary control on the size of an average leaf (Givnish, 1984; Richards, 1996). Mean annual precipitation is a proxy for available water that is both readily available from climate stations and applicable to a wide variety of research. The emphasis of this paper is therefore on the correlation between mean annual precipitation (MAP) and leaf morphology.

Recent paleoprecipitation estimates have been based on Wolfe's (1993) Climate Leaf-Analysis Multivariate Program (CLAMP), which ordinates a multivariate data set of leaf-morphologic characters scored from modern vegetational samples that are associated with climate stations to provide a quantitative framework for estimating climatic variables. The CLAMP samples are primarily from North American forests, and few are from the moist tropics. Estimates of MAP and other variables such as growing season precipitation have been derived either using CLAMP (Wolfe, 1994; Herman and Spicer, 1996, 1997) or multiple regression analysis of the CLAMP data set (Wing and Greenwood, 1993; Greenwood, 1996; Gregory and McIntosh, 1996). Most of these authors have noted the approximate nature of the statistical fits and urged caution when interpreting results. Only the multiple regression approach has been tested on living forests, with the result that both mean annual and growing season precipitation are consistently overestimated (Table 3.1).

An alternative to methods based on CLAMP is a reexamination of the positive univariate relationship between leaf area and annual precipitation (Webb, 1968; Dilcher, 1973; Dolph and Dilcher, 1980a, 1980b; Hall and Swaine, 1981; Givnish, 1984). Givnish (1984) quantified this relationship for a broad range of forest types in South America, Costa Rica, and Australia and found it to be significant. Preliminary tests of Givnish's equations with new data gave promising results, leading to the revised and expanded analysis presented here.

LEAF AREA AND PRECIPITATION

We selected fifty vegetation samples from living forests for our predictor set (Table 3.2), encompassing a wide variety of climates and vegetation. No samples were included from areas with few climate data, extreme winter cold and dry growing seasons, severe human modification, high salinity, or marked nutrient deficiencies. Samples with fewer than 16 species were excluded because above this value regression statistics were highly similar, but below about 16 species the fit deteriorated. Plants that were not native, dicotyledonous, woody, and leaf-bearing were excluded whenever they could be identified as such from species lists, as were mangroves, which typically inhabit saline environments. Ground herbs were uniformly excluded.

The mean of the natural logarithms of the species' leaf areas (MlnA) was estimated for each sample in either of two ways: directly from leaf-area measurements when possible, for seven samples, or, for the other 43 samples, from the proportions of species reported in each of the traditional Raunkiaer-Webb size categories (Raunkiaer, 1934; Webb, 1959; Fig. 3.1; Table 3.2). For compound leaves, leaflets were used instead of leaves. If two size classes were originally merged into one, separate values for the two size classes were log-interpolated.

For the direct measurement approach, we used either actual measurements of leaf area or length and width data from manuals, supplemented with U. S. National Herbarium material. For the latter, area values for each species were calculated as the mean of the natural log areas of the smallest and largest leaves, where leaf area was approximated as two-thirds length x width (Cain and Castro, 1959). The MlnA for the 43 samples scored with size categories was MlnA = $\sum a_i p_i$, where a_i represents the seven means of the natural log areas of the size categories (2.12, 4.32, 6.51, 8.01, 9.11, 10.9, and 13.1), and p_i represents the proportions of species in each category. Because the size classes are mostly a geometric series with a factor of nine, the lower bound of leptophyll was taken as the upper bound divided by nine, and the upper bound of megaphyll as the lower bound multiplied by nine (Givnish, 1984). This computation is similar to Givnish's "average width" (Givnish, 1984) and to the leaf size index (LSI) of Wolfe and Upchurch (1987). As a cross check, we converted the directly measured samples to Raunkiaer-Webb categories; changes in derived MlnA were small (maximum of 0.24).

The highly significant fit of MlnA as a function of mean annual precipitation is shown in Figure 3.2. The fit can be inverted for paleoclimatic purposes so that MAP is the dependent variable: ln(MAP) = 0.548 MlnA + 0.768, $r^2 = 0.760$, standard error = 0.359, $F(1,48) = 152$, $p = 10^{-15}$. We will refer to the application of the preceding as leaf-area analysis. The quality of fit is lower when ln(MAP) is regressed against LSI ($r^2 = 0.720$, $F = 124$).

We also compared the slope of the relationship of MAP as a function of the percentage of species with large leaves in our data set to that in the CLAMP data set of Wolfe (1993; Fig. 3.3). Because the percentages of species in the two largest size categories in CLAMP (Fig. 3.1) are values closely associated with moisture (Wolfe, 1993), a steeper slope in the CLAMP data set than in ours might explain the consistent pattern of overestimated MAP seen in Table 3.1. For the CLAMP data set, the percentage of large leaves was taken as the summed percentage of mesophylls 1 and 2 (Fig. 3.1) and for our data set as the summed percentage of mesophylls, macrophylls, and megaphylls. The comparison is not exact because the CLAMP mesophyll 1 category includes the upper part of the Raunkiaer-Webb notophyll category (Fig. 3.1).

The result of this mismatch should be that most CLAMP sites have a higher percentage of species with large leaves at a given MAP than do our sites, and that the slope in question is lower in the CLAMP data set than in our data set. Instead, the reverse is true: the slope within CLAMP is significantly higher (Fig. 3.3). We suggest that this steep slope causes overestimated mean annual precipitation (Table 3.1).

DISCUSSION

Leaf-area analysis, a univariate method, is more significant and has an r^2 close to or greater than those of various multivariate models based on the CLAMP data set (Wing and Greenwood, 1993; Gregory and McIntosh, 1996; Herman and Spicer, 1996). The benefits of using data from more than one major area are clear (Fig. 3.2). None of the six subsets of data covers the entire range of either axis, but the subtrends are subparallel. All but the Central American subset are primarily either above or below the trendline, which reflects some combination of differences in primary data collection and real variation among forests. For example, the low MlnA of the West Indian samples may result from the drying and destructive effects of high winds. The overall trend is probably not linear for the driest or the wettest climates, where biological stresses are maximized. At the dry end, MlnA appears to decline abruptly off the regression line (Fig. 3.2). Very wet climates typical of cloud forests were not sampled. Cloud forest leaves can be much smaller than leaves at lower and drier elevations in the same region (e.g., Howard, 1969). The lack of extreme values of MAP in our data set should therefore be noted by ecologists, but this omission is probably unimportant in the context of paleoprecipitation because desert and cloud forest floras are very rare in the fossil record.

The scatter in the regression (Fig. 3.2) mandates that leaf-area analysis be used with caution. Estimates based on several contemporaneous fossil samples are preferable to those from single samples. We strongly advise the use of supplemental data, including the distributions and characteristics of coals, clays, red-beds, and evaporites and the judicious analyses of fossil flora and fauna belonging to large extant clades with narrow moisture tolerances. Care must be taken with samples of fossil leaves to account for taphonomic removal of large leaves prior to deposition (Greenwood, 1992).

EOCENE EXAMPLE

Geological data have long indicated that the early to early middle Eocene of the U.S. Western Interior was much warmer than today, with generally frost-free winters (e.g., Roehler, 1993). Proxy paleoprecipitation data are critical for improving understanding of this unusual time period. Wing and Greenwood (1993) presented MAP estimates based on the CLAMP data set for six early and middle Eocene floras from the Western Interior and one from the West Coast, using two predictors, the percentages of species having (1) drip-tips and (2) leaves in the mesophyll 2 category (Fig. 3.1). The size categorizations were made from a data set of length and width measurements of the fossil leaves. Using these same data, we derived MlnA and reestimated paleo-MAP for the fossil samples with leaf-area analysis.

All seven revised estimates are lower (Table 3.3). The greatest change is for Bear Paw, which drops by more than half and is the only case where standard error bars of the original and revised estimates do not overlap; Bear Paw has the highest percentage of species with drip-tips (50%). The revised estimates rank in a logical fashion. Chalk Bluffs, California, emerges as the wettest sample, which is consistent with its being the only site near the coast. Green River, the youngest sample, ranks driest in both analyses, in accord with floristic evidence and vast evaporitic deposits in parts of the Green River Formation indicating intermittent dry periods (MacGinitie, 1969; Roehler, 1993). The Bear Paw, Sepulcher, Kisinger Lakes, and Wind River samples are intermediate both in age and in estimated MAP between the older Camels Butte and the younger Green River samples, possibly indicating a regional drying trend.

The revised estimates, although lower, all indicate much more humid conditions than are found at basinal elevations of the same areas today. Water vapor is the most significant of the greenhouse gases, contributing two to three times the atmospheric heat retention of carbon dioxide in the modern atmosphere (e.g., Bigg, 1996). Water vapor is also the agent of latent heat transport, a possible mechanism of continental warming in the early Eocene (Sloan et al., 1995). High humidity may help to explain the frost-free nature of early to middle Eocene climates in the western United States.

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TABLE 3.1. PRECIPITATION IN LIVING FORESTS, ESTIMATED FROM MULTIPLE REGRESSION ANALYSIS OF THE CLAMP DATA SET

Forest	Estimated (cm)	Actual (cm)
(1) Uganda, woodland	243*; 164†	124*; 60.5†
(2) Uganda, Mpanga rain forest	338*; 298†	136*; 45.9†
(3) Costa Rica, Santa Rosa National Park	212*; 207§	161*§
(4) Panamá, Barro Colorado Island	494*§	261*§
(5) Puerto Rico, Guánica Forest	162*§	86.0*§
(6) Pennsylvania, York County	260§	104*
(7) Pennsylvania, Allegheny National Forest	258§	116*

Notes: Uganda data from Jacobs and Deino (1996); Costa Rica data from Burnham (1997). Estimates (1-3) used multiple regression models of Wing and Greenwood (1993). Estimates (4-7) are from "subsamples" of Wilf (1997), multiple regression model of Wilf (1996).

*Mean annual precipitation.

†Three-month growing-season precipitation.

§Total growing season precipitation. For the Pennsylvania samples, mean annual precipitation is therefore estimated as > 258 cm.

TABLE 3.2. SUMMARY DATA FOR PREDICTOR SAMPLES

Sample	Mean annual precipitation (cm)	Mean ln (leaf area, mm^2)	Number of species measured
(1) SSA, Monte scrub	10-30	3.94	
(2) TSA, Thorn scrub	15-40	5.53	
(3) SSA, Arid Chaco woodland	30-40	4.50	
(4) TSA, Thorn forest	40-70	7.23	
(5) SSA, Western Chaco forest	45-70	5.85	
(6) Ghana, rainfall zone 1	50-75	7.62	17
(7) Jamaica, Cactus scrub	69	6.13	17
(8) Jamaica, Evergreen bushland	69	6.44	55
(9) SSA, Central Chaco forest	70-90	6.56	
(10) Puerto Rico, Guánica Forest	86	6.49	126
(11) Ghana, rainfall zone 2	75-100	7.77	94
(12) SSA, Transition forest	80-100	6.92	
(13) TSA, Deciduous forest	80-120	8.00	
(14) Pennsylvania, York County	104	7.79	56
(15) SSA, Eastern Chaco forest	90-120	6.82	
(16) Maryland, Smithsonian Environmental Research Center	111	8.27	27
(17) Jamaica, Dry evergreen thicket	112	7.23	58
(18) Ghana, rainfall zone 3	100-125	7.95	309
(19) St. John, woodland	113	6.63	173
(20) SSA, Gallery forest	100-130	6.86	
(21) Pennsylvania, Allegheny Ntl. Forest	116	7.72	47
(22) St. John, moist forest	120	6.95	227
(23) Ghana, rainfall zone 4	125-150	8.08	457
(24) Costa Rica site 7	151	7.86	30
(25) Costa Rica, Taboga	153	8.13	19
(26) Costa Rica site 5	160	8.02	25
(27) Costa Rica site 6	160	8.22	37
(28) Ghana, rainfall zone 5	150-175	8.15	495
(29) Costa Rica site 28	174	7.69	19
(30) Costa Rica site 29	174	7.95	16
(31) Costa Rica site 27	174	8.10	27
(32) Costa Rica site 25	185	8.90	23
(33) Ghana, rainfall zone 6	175-<200	8.23	375
(34) Nigeria, Omo Forest Reserve	208	8.62	
(35) Costa Rica site 32	248	7.64	30
(36) Costa Rica site 3	250	8.95	19
(37) Costa Rica site 22	253	8.91	21
(38) Costa Rica site 4	254	9.20	24
(39) Panamá, Barro Colorado Island	261	8.07	627
(40) Brazil, Mucambo, Belém	273	8.41	139
(41) Costa Rica site 21	293	8.46	20
(42) Costa Rica site 20	294	8.74	23
(43) Puerto Rico, Bisley Watersheds	350	7.95	131
(44) Costa Rica site 17	365	8.50	19
(45) Costa Rica site16	365	8.75	18
(46) Costa Rica site18	365	9.12	27
(47) Costa Rica, Osa secondary	430	9.29	18

TABLE 3.2

(48) Costa Rica, Osa ridge	435	8.47	18
(49) Costa Rica site 2	460	9.24	29
(50) Mexico, Los Tuxtlas	464	8.50	64

Notes: SSA = subtropical South America; TSA = tropical South America (Sarmiento 1972). When a range of annual precipitation was given, the midpoint value was analyzed (187.5 for Ghana zone 6). Number of species given when precisely known. Numbered Costa Rica sites correspond to site numbers in Dolph and Dilcher (1980a), climate data from Holdridge et al. (1971). Leaf areas for samples 10, 16, 19, 22, 39, 43, and 50 calculated from direct measurements; otherwise from size categories. Samples 14 and 21 are “subsamples” of Wilf (1997); samples 10, 19, 22, 39, and 43 are “samples” of Wilf (1997). Ghana data: Hall and Swaine (1981); Jamaica: Loveless and Asprey (1957); Puerto Rico: Little and Wadsworth (1964); Little et al. (1974); Acevedo-Rodríguez and Woodbury (1985); Chinea et al. (1993); Maryland: unpublished data furnished by G. Parker; St. John: Acevedo-Rodríguez (1996); Costa Rica samples 25, 47, 48: Gentry (1969); Dolph and Dilcher 1980b; Nigeria: Richards (1939, 1996); Panamá: Croat (1978); Brazil: Cain et al. (1956); Mexico: Bongers et al. (1988); Bongers and Popma (1990).

TABLE 3.3. ESTIMATED MEAN ANNUAL PRECIPITATION FOR SEVEN EARLY AND MIDDLE EOCENE FLORAS

Flora (Ma)*	Wing and Greenwood (1993) (cm)[†]	This paper (cm)[§]
Bear Paw (49-51)	277	130 +56.1,-39.2
Sepulcher (50-51)	195	136 +58.8,-41.0
Camels Butte (53-55)	162	157 +67.6,-47.2
Chalk Bluffs (50-52)	241	160 +68.9,-48.1
Green River (45-48)	116	84 +36.2,-25.3
Kisinger Lakes (49-50)	129	110 +47.4,-33.1
Wind River (50-51)	149	104 +44.8,-31.3

*Age estimates from Wing and Greenwood (1993).

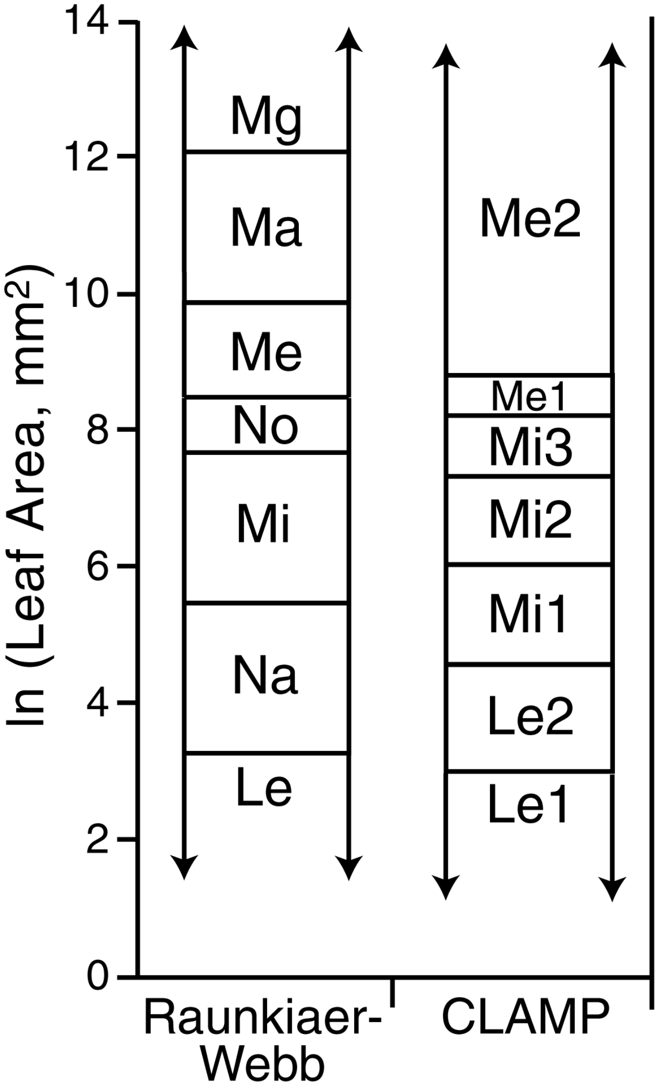
[†] Standard error is ±58.0 cm.

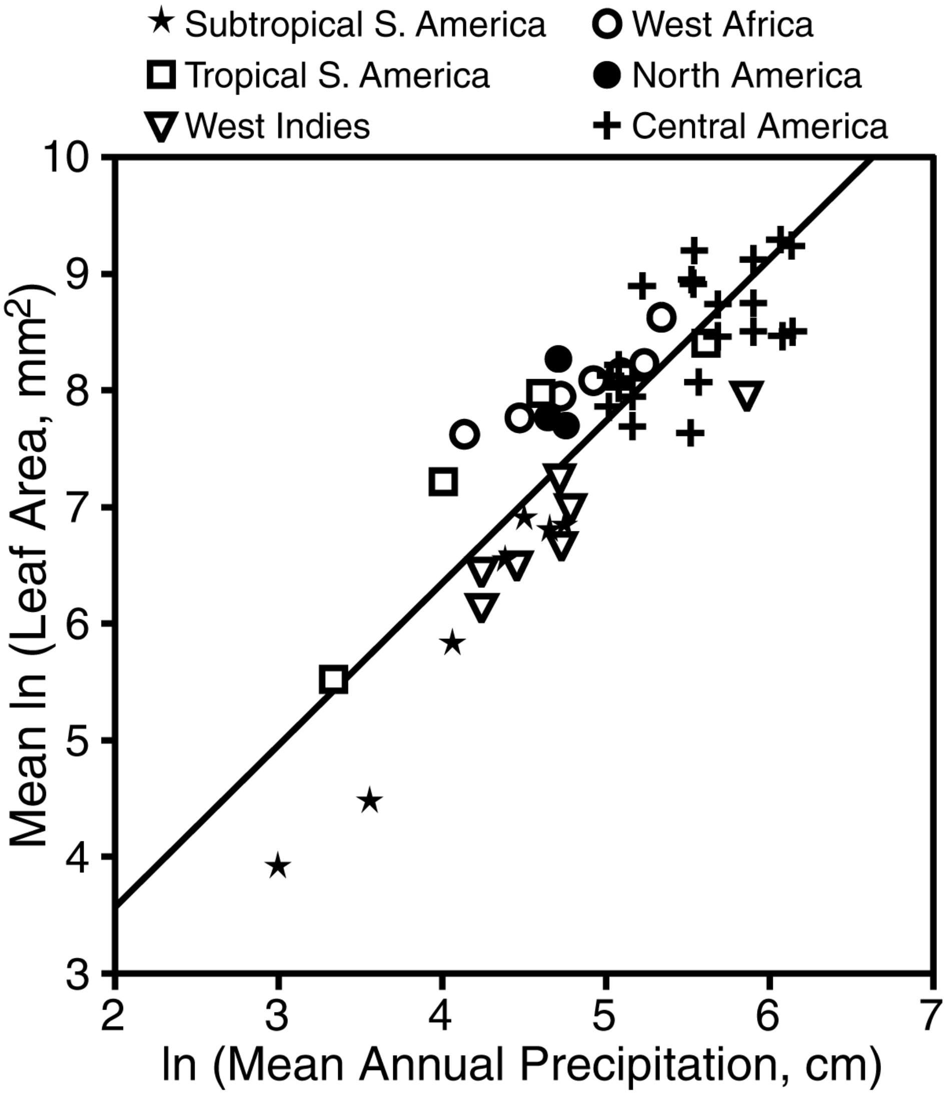
[§] Single standard errors shown are asymmetrical because they were converted from logarithmic units.

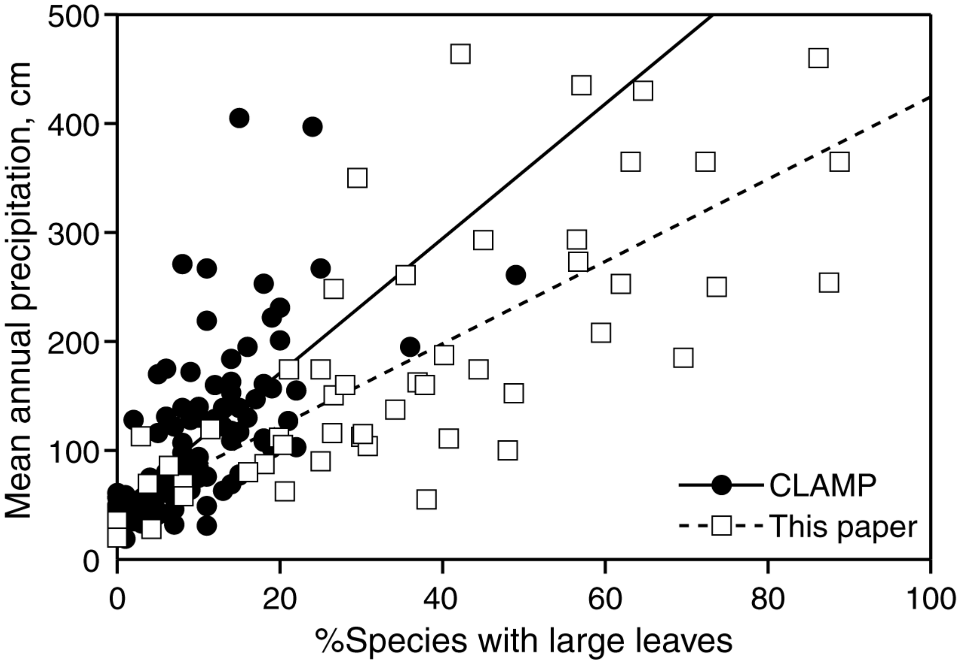
Figure 3.1. Two systems of leaf-area classification, shown on natural log scale: Raunkiaer-Webb (Webb, 1959) and CLAMP (Climate Leaf-Analysis Multivariate Program: Wolfe, 1993). CLAMP sizes were measured from Wolfe (1993, p. 25) using digitizing tablet. Abbreviations: Le = leptophyll, Na = nanophyll, Mi = microphyll, No = notophyll, Me = mesophyll, Ma = macrophyll, Mg = megaphyll (Le1 = “leptophyll 1”, etc.). Cutoff values (in mm^2): 25, 225, 2025, 4500, 18225, 164025 (Raunkiaer-Webb); 19, 91, 392, 1420, 3516, 6226 (CLAMP).

Figure 3.2. Mean natural log leaf area (MlnA) as a function of mean annual precipitation (MAP): MlnA = 1.39 ln(MAP) + 0.786, $r^2 = 0.760$, standard error = 0.572, F (1,48) = 152, $p = 10^{-15}$. Data from Table 3.2.

Figure 3.3. Regressions of mean annual precipitation (MAP) vs. percent of species with large leaves for the CLAMP data set (Wolfe 1993) and the leaf-area analysis data set of this paper (Table 3.2). For CLAMP: MAP = 6.18(%mesophyll 1 + %mesophyll 2) + 47.5, $r^2 = 0.439$. For leaf-area analysis: MAP = 3.77(%mesophylls + %macrophylls + %megaphylls) + 47.0, $r^2 = 0.554$. The difference in slope is significant at the $p < 0.001$ level, using the equality test of Sokal and Rohlf (1995: p. 498).


ln (Leaf Area, mm²)
14
12
10
8
6
4
2
0
Mg
Ma
Me
No
Mi
Na
Le
Me2
Me1
Mi3
Mi2
Mi1
Le2
Le1
Raunkiaer-Webb
CLAMP


★ Subtropical S. America
○ West Africa
□ Tropical S. America
● North America
▽ West Indies
✚ Central America
Mean ln (Leaf Area, mm²)
ln (Mean Annual Precipitation, cm)
10
9
8
7
6
5
4
3
2
3
4
5
6
7


Mean annual precipitation, cm
0
100
200
300
400
500
0
20
40
60
80
100
%Species with large leaves
CLAMP
This paper

CHAPTER FOUR

PORTRAIT OF A LATE PALEOCENE (EARLY CLARKFORKIAN) TERRESTRIAL ECOSYSTEM: BIG MULTI QUARRY AND ASSOCIATED STRATA, WASHAKIE BASIN, SOUTHWESTERN WYOMING

This chapter is written in the style of the journal *Palaios*, where it has been accepted for publication. Coauthors K. C. Beard and J. W. Norejko contributed the faunal analyses. Coauthor K. S. Davies-Vollum contributed the sedimentological analyses.

Portrait of a Late Paleocene (Early Clarkforkian) Terrestrial Ecosystem: Big Multi Quarry and Associated Strata, Washakie Basin, Southwestern Wyoming

PETER WILF
Department of Paleobiology, MRC 121, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560
K. CHRISTOPHER BEARD
Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213
K. SIÂN DAVIES-VOLLUM
Department of Geology, Ball State University, Muncie, IN 47306
JAY W. NOREJKO
Department of Anatomical Sciences, State University of New York at Stony Brook, Stony Brook, NY 11794

In-depth understanding of past climatic and biotic change requires the study of ancient ecosystems. However, terrestrial plants and vertebrates are preferentially preserved under very different taphonomic conditions, and diverse fossil floras and faunas are rarely found in close association. Big Multi Quarry and associated strata in the uppermost Fort Union Formation of the Washakie Basin, southwestern Wyoming, provide a uniquely detailed record of terrestrial fauna, flora, and climate during the early Clarkforkian. The Clarkforkian Land Mammal Age, approximately the last million years of *the Paleocene, was an interval of global warming that had profound biotic consequences.*

The mammalian fauna of Big Multi Quarry, consisting of 41 species, is the most diverse known from a single Clarkforkian locality. Unlike most other Clarkforkian faunas, the Big Multi Quarry assemblage is not significantly biased against small forms. Lipotyphlan insectivores were dominant, and arboreally adapted taxa were abundant and diverse. The closely associated and well-preserved fossil plant assemblage was overwhelmingly dominated by a single species belonging to the birch family. Floral richness, heterogeneity, and evenness were as low as in the Tiffanian of the same region, showing that forest structure remained monotonous even as climate warmed and mammals diversified in the Clarkforkian. The plant assemblage more closely resembles middle than early Clarkforkian floras of northern Wyoming, suggesting northward migration of the ranges of plant taxa coincident with warming.

A great deal of research has focused on the unusually warm interiors of continents in the terminal Paleocene and early Eocene. Multiple lines of evidence from our study, including sedimentological indicators, analyses of the nearest living relatives and functional analogues of the fossil plants and animals, size and margin analysis of fossil leaves, and cenogram analysis of the mammalian fauna, indicate that well before the terminal Paleocene southwestern Wyoming had a humid subtropical climate with little or no seasonal frost or marked dry season.

INTRODUCTION

The Clarkforkian North American Land Mammal Age (NALMA), approximately the last million years of the Paleocene (Butler et al., 1981; Berggren et al., 1995), was an interval of global warming that linked the cooler earlier Paleocene with the hothouse of the early Eocene (Savin, 1977; Corfield and Cartlidge, 1992; Zachos et al., 1994; Wing et al., 1995, 1999). As a result of this sustained warming trend, at least three successive waves of Asian endemic mammals were able to disperse into North America across a high-latitude filter that probably coincides with present-day Beringia (Beard, 1998). The first of these waves, consisting of archaic herbivorous mammals known as uintatheres (Dinocerata) and arctostylopids, arrived in the latter part of the preceding Tiffanian NALMA (zone Ti5 of Archibald et al., 1987). The second and third waves of immigrants bracket the Clarkforkian NALMA itself. The beginning of the Clarkforkian is defined by the first North American appearances of rodents, coryphodontids (Pantodonta), and tillodonts. The Clarkforkian is also associated with a floral immigration in the Northern Rockies, where many arriving taxa had modern subtropical to tropical affinities and were predominantly evergreen, including members of the cycad, ginger, laurel, and tea families (Hickey, 1980; Wing, 1998). The beginning of the succeeding Wasatchian NALMA is defined by the arrival of the third wave of immigrants, which included even-toed and odd-toed ungulates (Artiodactyla and Perissodactyla, respectively), lemur-like and tarsier-like primates, and the carnivorous hyaenodontids. Immigrant plant genera in the earliest Wasatchian of the Northern Rockies included *Platycarya*, *Alnus* (alder), the scrambling fern *Lygodium*, the aquatic fern *Salvinia*, and the tree fern *Cnemidaria* (Hickey, 1977; Wing, 1998; Wing et al., 1999). The Clarkforkian, therefore, records part of this iterative pattern of immigration and the initial response of the native North American biota, both of which were mediated by climatic warming.

Despite the importance of the Clarkforkian for understanding the mechanisms and effects of global warming on land, nearly all work to date on a fine stratigraphic scale has focused on a single area, the Bighorn Basin of northwestern Wyoming (Hickey, 1980; Gingerich et al., 1980; Rose, 1980, 1981a; Archibald et al., 1987; Bown et al., 1994; Wing, 1998; Wing et al., 1995, 1999). This geographic restriction limits our ability to understand whether patterns seen in the Bighorn Basin reflect local, regional, or global processes. Moreover, biogeographic consequences of climate change can only be understood by examining records from more than one area.

The most significant Clarkforkian mammal locality outside of the Bighorn Basin is Big Multi Quarry, located in the Washakie Basin (Fig. 4.1), about 350 km south of the classic Clarkforkian sections in the Bighorn Basin (Gingerich et al., 1980; Rose, 1981a). Fossil mammals from Big Multi Quarry comprise the most diverse Clarkforkian mammal fauna yet obtained from a single locality. Because of unusually thorough faunal sampling, Big Multi Quarry is ideally suited for reconstruction of ancient climate and habitats using methods that rely on faunal data. Furthermore, the fauna is associated with a well-preserved fossil plant assemblage, both in the bedding planes immediately above the quarry and throughout a well-exposed local section of 18 m. The plant assemblage is sufficient for reconstruction of paleoclimate and paleoecology, and sedimentological data provide additional information on paleoclimate and paleoenvironment.

The purpose of this paper is to integrate these different lines of evidence regarding the Clarkforkian biota, climate, and environment of southwestern Wyoming. The picture that emerges is the most complete portrait now available of a Clarkforkian terrestrial “ecosystem”. At the same time, the record from Big Multi Quarry and associated strata broadens the geographic coverage of our understanding of this important interval.

Setting

The study area is located near the settlement of Bitter Creek, Sweetwater County, Wyoming, in the northwestern Washakie Basin, a sub-basin of the Greater Green River Basin (Fig. 4.1). Today this area is an arid and windy high desert, with less than 30 cm of annual rainfall, January mean temperature near -10°C, and only about 100 frost-free days per year (Knight, 1994). Big Multi Quarry lies in the uppermost part of the Fort Union Formation, which crops out around the trace of the Rock Springs Uplift (Love and Christiansen, 1985). Along the eastern flank of the Rock Springs Uplift, the thickness of the Fort Union Formation varies from about 420 to 750 m (Roehler, 1979; Winterfeld, 1982; Hettinger and Kirschbaum, 1991). Fort Union strata in this region do not provide a continuous record of Paleocene deposition. Rather, stratigraphic unconformities correspond to temporal hiatuses across the Cretaceous/Tertiary boundary and within the early and middle Paleocene (Roehler, 1979; Winterfeld, 1982; Kirschbaum and Nelson, 1988; Kirschbaum et al., 1994). Fossil mammals demonstrate local Fort Union deposition during the late Torrejonian (To3) and latter Tiffanian (Ti4-Ti5) NALMAs (Winterfeld, 1982), in addition to the Clarkforkian interval emphasized here. The overlying Wasatch Formation contains vertebrates representing the Wasatchian NALMA (Gazin, 1962; Savage et al., 1972; Savage and Waters, 1978; Williams and Covert, 1994). The Fort Union-Wasatch contact is locally covered by alluvium, approximately 80 m above Big Multi Quarry.

Big Multi Quarry occurs in a 0.5-m-thick, purple-gray, blocky mudstone near the base of our 23.4-m measured section (Figs. 4.2, 4.3). The vertebrate-bearing horizon is laterally continuous and traceable for at least 100 m. The local section is well-exposed by ephemeral drainages but bounded by covered intervals. Lithologies consist of coarsening-up packages of dark coal, rooted and drab underclay, carbonaceous shale, siltstone, progressively coarser grades of muscovitic sandstone, including cross-bedded strata, and limy siltstones. The limy siltstones are the most resistant units, and their weathered and fractured remains typically cap small buttes in the area. There are no mature paleosols, downcut channels, or any other indications of significant unconformities in the local section. Redbeds are absent, and rocks in general are drab-colored. The only exceptions are the purple coloration of the mudstone comprising Big Multi Quarry, an orange-stained goethitic sandstone immediately above the quarry, and yellow coloration from natrojarosite associated with coals. Paleosols in the area are thin, rooted underbeds lacking differentiated horizons as well as carbonate nodules. Poorly preserved fossil wood is common as talus. The lithologies observed in our section are typical of the upper Fort Union Formation throughout its outcrop zone around the Rock Springs Uplift (Roehler, 1973, 1979; Kirschbaum, 1987; Hettinger and Kirschbaum, 1991).

Plant compression-impression megafossils, primarily of leaves, are abundant in carbonaceous shales, siltstones, and sandstones throughout the local section (Fig. 4.3), especially at two stratigraphic levels: (1) immediately above Big Multi Quarry in gray and orange siltstone and sandstone (Fig. 4.2); and (2) in a 0.5-m-thick carbonaceous shale and 0.5-m siltstone unit that occurs from 18 to 19 m above Big Multi Quarry, where plant species diversity is highest and preservation is best (hereafter referred to as the “18-m level”). The latter is interpreted as a swamp deposit; it is laterally extensive and bears fossil plants over a distance of 1.3 km along strike. Given the conformable and floristically uniform nature of the local section, it is reasonable to assume that the 18 m of section from Big Multi Quarry to the best fossil plant horizon covers a very short interval of geologic time and that the fossil vegetation can be combined for analysis. The 18 m represents less than 40 ky if sedimentation rates recently calculated for the Clarkforkian of the Clark's Fork Basin are roughly applicable (Wing et al., 1999).

Previous work

Big Multi Quarry was discovered in 1976 by a field party from the University of California Museum of Paleontology (UCMP) under the direction of Dr. Donald E. Savage (UCMP loc. V76134). According to Rose (1981a: p. 131), the locality derives its name from the discovery of a large multituberculate (?*Neoliotomus*) during initial field work. Unfortunately, the relevant specimens were misplaced soon thereafter, and the exact identity of the large multituberculate remained a mystery for many years. However, the original multituberculate specimens were recently rediscovered in the UCMP collections and can now be provisionally referred to *N. conventus*. Based on the 1970s collections, Rose (1981a, p. 131-132) provided an annotated faunal list for Big Multi Quarry consisting of some 25 species of mammals. Citing the presence of *Plesiadapis cookei*, Rose (1981a) correlated the assemblage with the middle Clarkforkian (Cf2) *Plesiadapis cookei* Zone of the Bighorn Basin. However, we regard the occurrence of *P. cookei* at Big Multi Quarry as questionable because we have not found specimens of *P. cookei* in either the Berkeley or subsequent collections.

In 1992, field parties from the Carnegie Museum of Natural History (CM) resumed work at Big Multi Quarry, which has now been excavated intensively for six consecutive field seasons (CM loc. 2433). This new phase of research has significantly expanded our knowledge of the fauna, which now consists of 41 species of mammals. Two new species of rodents from Big Multi Quarry, among the oldest known from North America, were described by Dawson and Beard (1996). These included the first North American species of the primitive rodent family Alagomyidae, otherwise known only from early Cenozoic localities in Mongolia and China (Dashzeveg, 1990; Meng et al., 1994; Tong and Dawson, 1995). Systematic study of the remainder of the mammalian fauna is ongoing.

Plant fossils have occasionally been reported from the upper Fort Union Formation of the Rock Springs Uplift (Brown, 1962; Roehler, 1979; Kirschbaum, 1987), but few paleobotanical publications have treated this area and time period in any depth. Most research has been systematic (Manchester and Chen, 1996; Manchester and Dilcher, 1997). Gemmill and Johnson (1997) recently published a paleoecological analysis of a Tiffanian plant assemblage from the nearby Great Divide Basin. Their work was conducted at similar spatial scales to ours, consisting of ten localized sediment samples collected over a limited total area, thus providing a useful temporal antecedent to this study. Field crews from the U.S. National Museum of Natural History (USNM) conducted the paleobotanical field work for this study during the 1994-1996 field seasons.

Kirschbaum et al. (1994) showed that prevailing paleocurrents in the area were southerly, with the crystalline Wind River Mountains to the north supplying lithic sand, and that these drainages eventually joined northward-flowing drainages from the Uinta Mountain Front before flowing east. The Rock Springs Uplift in the latest Paleocene was flattened by erosion and did not impede this drainage pattern (Kirschbaum et al., 1994). The only previous paleoclimatic report is that of Roehler (1979), who suggested, on the basis of lithologic observations and preliminary collections of fossil leaves, pollen, and vertebrates from correlative rocks in the adjacent Sand Butte Rim NW Quadrangle, that "...the (Fort Union) rocks were deposited in a subtropical climate in swamps and on forested floodplains, probably not more than 900-1300 ft. above sea level."

METHODS

Sedimentological Analysis

The section shown in Figure 4.3 was measured from below the base of the vertebrate-bearing mudstone, to USNM loc. 41264 (4-m level), USNM loc. 41276 (11-m level), and USNM loc. 41271 (18-m level), ending at the siltstone cap on the butte containing the latter locality. In addition, detailed sedimentological logs were taken of the major fossiliferous layers, at Big Multi Quarry and at four localities along the strike of the 18-m plant bed, one of which is shown in Figure 4.3. These logs identified beds on the centimeter scale to detect minor changes in lithologies and deposition. Each bed was assessed for thickness, type of boundary with adjacent beds, Munsell color, grain size, sedimentological features, structure, presence and type of organic material, and coloration by secondary and pedogenic minerals. Representative samples from each of the fossil-bearing beds were collected for analysis of total organic carbon content (TOC; Table 4.1). These were taken from well below the weathered surface to avoid errors associated with the introduction of modern organic material. To evaluate TOC, we used low-temperature combustion methods (Wilde et al., 1979), where TOC is equal to the weight of carbon divided by the dry weight.

Specimen Collection and Processing

The most complete specimens of fossil vertebrates were invariably collected by small-scale quarrying, either by hand or using hand-held tools. However, in order to sample the fauna as thoroughly as possible and to remove collecting biases against the recovery of small taxa, virtually all fossiliferous rock was screen-washed subsequent to initial quarrying. Some specimens were also obtained by surface-prospecting, amounting to fewer than 1% of all specimens recovered.

Plant megafossils were collected from 15 quarries at four stratigraphic levels (Fig. 4.3, Table 4.2). Each quarry comprised only 1-2 m^3 of sediment in order to allow investigation of small-scale variation in vegetation. Collections representing the full range of morphological variation found for each species at each locality have been deposited at USNM under accession no. 420051. Fossil plants were segregated into morphospecies (Table 4.2) based on previous descriptive work and detailed analysis of the leaf architecture of undescribed forms (Hickey, 1973, 1979; Hickey and Wolfe, 1975).

Paleoecology

Both the vertebrate and plant assemblages appear to be parautochthonous and therefore well suited for paleoecological study. The frequent preservation of delicate, yet relatively complete microvertebrate fossils strongly indicates minimal transport. This interpretation is consistent with the fine-grained sediments comprising the vertebrate-bearing bed, which imply a low-energy depositional environment. The relative abundance of mammals in small, medium, and large size classes closely approximates that in a modern woodland assemblage (Fig. 4.4), suggesting that sampling bias against any particular size class is negligible. Most other Clarkforkian mammal assemblages are dominated by medium and large-bodied taxa (Rose, 1981a). Also, it is widely acknowledged that fossil assemblages produced by surface collecting, including the vast majority of Clarkforkian assemblages currently known, are systematically biased against the recovery of small taxa (e.g., Winkler, 1983). Our collecting methods were designed to allow the small mammal component to be sampled especially thoroughly. Hence, we argue that the Big Multi Quarry assemblage provides the most unbiased approximation of a Clarkforkian mammalian community currently available.

Preservation of plant fossils is good to excellent. Fine details of leaf architecture are commonly preserved, often including the highest orders of venation. Cuticular preservation occurs on many specimens. Leaves from the 18-m level are of many different sizes on the same slab, indicating little taphonomic sorting. Davies-Vollum and Wing (1998) have shown that plant fossils found in fine-grained sediments of backswamp environments similar to those at the 11-m and 18-m levels preserve parautochthonous floral assemblages. Plant fossils found in coarser-grained sediment in the section, such as at the 1-m and 4-m levels, may have been transported short distances under higher energy fluvial conditions. The coarse-grained rocks indicate environments that were subject to more frequent sediment influx, as individual leaf layers tended to be separated vertically by sand, while the finer-grained sediments at the 18-m level produced more leaf mats. However, even in these coarser-grained sediments, the preservation of fine detail and the lack of mechanical damage indicate that there was not substantial transport prior to deposition. In addition, the presence of roots below plant beds throughout the section shows that standing phytomass was present (Fig. 4.3). For the fossil leaves to be derived from a distant source, they would have to be transported into the area in large numbers and also displace the leaf litter of existing forests.

All mammal specimens identifiable to the species level were tabulated (Table 4.3), yielding measures of relative abundance of the mammalian fauna in the form of total number of specimens (TNS) and minimum number of individuals (MNI). It is widely thought that MNI overestimates the abundance of rare species but underestimates the abundance of common forms (e.g., Rose, 1981b, and references therein). Although estimates of relative abundance based on TNS and MNI varied somewhat, these differences were typically minor (Fig. 4.4, Table 4.3). Diversity indices were calculated for comparison with similar data for other Paleocene and early Eocene North American mammal faunas taken from the literature (Table 4.4).

For the plants, the primary paleoecological technique was field censusing (Table 4.5). Our methodology was very similar to that of Gemmill and Johnson (1997) and Davies-Vollum and Wing (1998). Actualistic study in modern forests by Burnham et al. (1992) has shown that there is a strong positive correlation between the leaf mass of species recovered from litter baskets and the stem basal area of the source forest, that a correlation nearly as strong exists when leaf area is used instead of leaf mass, and that leaf count is a good proxy for leaf area. This study and others have shown that individual, highly local litter samples reflect the species composition of a source area of no more than about 20 m radius (Burnham, 1996, 1997). Burnham et al. (1992) suggested that, for minimally transported samples of fossil vegetation, censuses of 350-400 leaves would provide a useful approximation of the relative stem biomass of the ancient plant species in the immediate vicinity and would probably recover most of the species that shed leaves into the depositional site. The goal in this study was at least 350 leaves per site, but this number was lowered slightly if site richness was very low or raised if the site was more diverse. Non-dicots were not counted because their foliage was fragmentary. Diversity indices were calculated for the censused quarries (Table 4.5). To the extent that leaf counts reflect relative dominance of species in the source forest, diversity indices based on leaf counts directly reflect evenness and concentration of dominance within the original biomass.

Paleoenvironmental and Paleoclimatic Analysis from Fossils

Vertebrates

Data from fossil vertebrates can be used to infer aspects of ancient environments and climates, although paleobotanical data are frequently regarded as more reliable indicators. We used two different methods. The first relies on assessment of the habitat preferences and/or requirements of nearest living relatives (NLRs); the second is a semi-quantitative approach known as cenogram analysis.

The NLR approach has greatest potential when phylogenetic relationships are well established, identification of fossils is nonproblematic, and the living relatives of fossil forms remain diverse and widespread, with environmental requirements that are well documented (e.g., Markwick, 1994). We assume that the precision and accuracy of the NLR approach decreases as a function of the age of the fauna under analysis. However, even when phylogenetic affinities with living taxa are either remote or poorly established, as is typically the case for Paleocene mammals, it may still be possible to draw paleoenvironmental inferences on the basis of reconstructed functional or ecological attributes of fossil taxa. For example, taxa that are thought to have been arboreal for purely anatomical reasons imply the presence of forested or at least woodland conditions.

The cenogram method is based on the empirical observation that the distribution of body size among non-carnivorous and non-volant species comprising modern mammalian faunas varies in specific ways with respect to environmental moisture and habitat regime (Legendre, 1989). Several workers have applied cenogram analysis to Paleogene mammal faunas (e.g., Gingerich, 1989; Legendre, 1989; Gunnell, 1994, 1997; Gunnell and Bartels, 1994). Because cenogram analysis is based on body-size distribution across the entire mammalian fauna, its application to fossil assemblages is only appropriate when most or all of the ancient fauna is believed to have been sampled and when a variety of collecting methods have been employed to minimize the problem of taphonomic bias (cf. Gunnell, 1994). Given its unusually high diversity of mammalian species and the variety of sampling procedures used, the Big Multi Quarry sample probably comes closer to meeting these criteria than most Paleocene mammal assemblages in North America.

Cenograms are dependent on accurate estimates of body mass, which are typically obtained using regressions of body mass versus lower first molar (M_1) area in various mammalian groups (Legendre, 1989). Many North American Paleocene mammal taxa belong to extinct groups having uncertain phylogenetic relationships. Hence, it is frequently unclear which of these different regression models is most appropriate. In such cases, we usually employed Legendre's (1989) most generalized, "all mammal" regression model (Table 4.3). However, unique problems arise in estimating the body mass of extinct taxa, such as multituberculates and palaeanodonts, that are dentally highly specialized and for which the scaling properties of M_1 area with respect to body mass remain entirely unknown. Gunnell (1994) excluded multituberculates from his cenogram analyses of Paleocene mammal faunas in North America because of difficulties in relating M_1 area to body mass. While we are fully aware of this problem, we have nonetheless included multituberculates in our cenogram analysis, on the theory that using an imperfect estimate of body mass in multituberculates is preferable to ignoring such a significant component of the mammalian fauna altogether. Body mass in multituberculates was estimated using Legendre's (1989) "all mammal" regression of body mass versus M_1 area, with M_1 area in multituberculates adjusted by a factor of 0.5

to compensate for the hypertrophy of M_1 in this taxon. Similarly, body mass of *Palaeanodon* sp., cf. *P. parvulus* was estimated as 750 g by comparison with its larger relative *Brachianodon westorum*, the body mass of which was estimated by Gunnell and Gingerich (1993) to lie between 1.0 and 2.7 kg.

Plants

Fossil plants have long been recognized for their potential to indicate past climates (e.g., Lesquereux in Hayden, 1871, p. 374). We employed two approaches: (1) analysis of the climatic preferences of the NLRs of the fossil vegetation, and (2) the uniformitarian application of the correlation of the sizes and shapes of modern leaves to prevailing climatic conditions. The relative advantages and disadvantages of each approach have been exhaustively compared elsewhere (e.g., Wing and Greenwood, 1993; Herman and Spicer, 1997), and the potential pitfalls inherent in the NLR approach, discussed above with respect to fossil vertebrates, apply to plants as well. In contrast to the use of NLRs, quantitative methods based on dicot leaf size and shape are theoretically independent of taxonomy (Wolfe, 1979, 1993). The two strongest leaf-climate relationships currently known are the positive correlations of (1) mean annual temperature (MAT) and the proportion of woody dicot species with entire (untoothed) margins (Wolfe, 1979; Wilf, 1997), and (2) mean annual precipitation (MAP) and leaf area (Givnish, 1984; Wilf et al., 1998). Use of these correlations to estimate past mean annual temperature and mean annual precipitation is known as leaf-margin analysis and leaf-area analysis, respectively, and these two methods are employed here (Table 4.6). The equation for leaf-margin analysis is Wing and Greenwood's (1993) quantification of Wolfe's (1979) East Asian dataset:

$$\mathrm{MAT} = 30.6P + 1.14,$$

where *P* is the proportion of species of woody dicotyledons that have entire margins. The same equation has been used for recent paleo-MAT estimates from Clarkforkian floras of the Bighorn Basin, allowing a firm basis of comparison (Wing et al., 1999). The equation for leaf-area analysis is

$$\ln (\mathrm{MAP}) = 0.548\ \mathrm{MlnA} + 0.768,$$

standard error = 0.359, where MAP is in centimeters and MlnA is the mean of the natural logs of the species' leaf areas, area measured in square millimeters (Wilf et al., 1998).

Our leaf-margin and leaf-area data are based on the 20 presumably woody dicot leaf types found in the local section. To ascertain whether these taxa were a representative sample of the fossil flora over a broader area or a locally biased assemblage, we examined 22 roughly contemporaneous quarries of the uppermost Fort Union Formation on the east and south flanks of the Rock Springs Uplift (Wilf, unpublished data), adding several thousand specimens. Remarkably, these additional sites added only three leaf types (two toothed, one untoothed). The Big Multi local section, therefore, holds most of the dicot richness that can be recovered in the region and is clearly representative. For leaf-area analysis, we used the full range of leaf area found for each local taxon over the entire late Paleocene of the Rock Springs Uplift in order to take advantage of the additional sampling (Wilf, unpublished data). After Wilf et al. (1998), we calculated MlnA using the Raunkiaer-Webb system of discrete leaf areas (Webb, 1959). No upward adjustment in MlnA was made for possible removal of large leaves prior to deposition (Greenwood, 1992; Gregory and McIntosh, 1996), for several reasons. First, all of the samples were intensively collected over a large area, so that at least for common species, the largest leaves are likely to have been recovered. Second, analyses of leaf fossil-sediment relationships and comparison with recent taphonomic studies (Davies-Vollum and Wing, 1998) strongly indicate that most of the plant fossils were minimally transported. Third, there is no correction factor that has been shown to improve estimates of original leaf area.

BIOTA

Composition and Richness

With 41 species, Big Multi Quarry is richer than any other Clarkforkian mammalian assemblage (Table 4.3). Composition generally conforms with that of other well-sampled Clarkforkian faunas (Rose, 1981a, 1981b; Krause, 1986). Small insectivorous taxa dominate the assemblage, but relatively large herbivorous forms such as *Phenacodus* and *Probathyopsis* are also represented. As is typical of Paleocene mammal faunas in North America, most taxa belong to archaic groups without clear phylogenetic ties to modern orders. The marsupial *Peradectes*, the rodents *Paramys* and *Alagomys*, the carnivorans *Didymictis* and *Viverravus*, and the hedgehog *Leipsanolestes* are among the only mammals that can be unambiguously referred to modern higher taxa, although distant relatives of living Southeast Asian flying lemurs (order Dermoptera) are represented by *Phenacolemur*, cf. *Ignacius*, *Tinimomys*, *Chalicomomys*, and various plesiadapoid genera (Beard, 1990, 1993a, 1993b). Several groups that occur elsewhere in the western U.S. during this interval have not yet been recorded at Big Multi Quarry. These taxa include mesonychids, arctostylopids, oxyaenid creodonts, the hyopsodontid condylarth *Haplomylus*, and the pantodont *Coryphodon*. Mesonychids, arctostylopids, and oxyaenids are rare elements of penecontemporaneous mammalian faunas (Rose, 1981a, 1981b). Their absence at Big

Multi Quarry may be an artifact of sampling, despite intensive efforts to overcome this problem.

A diverse herpetofauna, including salamanders, turtles, lizards, a champsosaur, and crocodilians, has been recovered from Big Multi Quarry, but these taxa have not yet been studied in detail. Among the crocodilians, both *Allognathosuchus* and *Ceratosuchus* have been identified (Rose, 1981a, p. 139).

Plant species richness is comparable to other localized plant assemblages in the late Paleocene of the Rocky Mountains. Gemmill and Johnson (1997) reported 28 leaf morphotypes for the Tiffanian Bison Basin florule from the Great Divide Basin, versus 27 in our sample, with a maximum at any one quarry of 14 leaf types, versus 13 in our section (Table 4.2). The Almont assemblage of North Dakota (Crane et al., 1990), which is probably Clarkforkian in age, was also collected over a small area and yielded a total of 24 leaf types. The overlying and presumably Clarkforkian Bear Den Member of the Golden Valley Formation, collected over a large area, has produced fewer than 25 leaf types (Hickey, 1977). The most speciose locality in the early Clarkforkian of the Clark's Fork Basin, Double Kill Hill, yielded 25 species (Wing et al., 1995). The low species richness in our section is therefore typically Paleocene and not a taphonomic artifact.

Fossil vegetation from the coarsening-up sequence immediately above Big Multi Quarry is not particularly species-rich (Table 4.2). Families that can be recognized with reasonable confidence are the Betulaceae (birch family), Cornaceae (dogwood family), Lauraceae (laurel family), Zingiberaceae (ginger family), Taxodiaceae (bald cypress family), and a probable member of the Cercidiphyllaceae (katsura family). *Palaeocarpinus aspinosa* co-occurs with its presumed leaf type, *Corylites* (Manchester and Chen, 1996). "*Cinnamomum" sezannense, "Ficus" planicostata*, FW27, and

Calycites sp. are the only forms restricted to this part of the section, most local to the mammal quarry.

When the upper part of the section is added (Table 4.2), the additional elements include leaf types of the Magnoliaceae (magnolia family) and Juglandaceae (walnut family), the guava berry *Paleomyrtinaea* (Pigg et al., 1993), undoubtedly a food source for vertebrates, and several non-dicots, including fragmentary palm leaves (*Amesoneuron*), *Metasequoia*, the ferns *Allantodiopsis erosa* and *Woodwardia gravida*, and a horsetail (*Equisetum*).

Insect-feeding damage on fossil leaves is ubiquitous throughout the section and exhibits some host specificity. Types of damage observed are two types of hole feeding, margin feeding, at least two galling types, window feeding, skeletonization, and at least four types of mines, some with well-preserved frass trails (terminology *sensu* Beck et al., in press). Gastropod shells are abundant within the mudstone bearing the mammals (Fig. 4.3). A single pulmonate examined may belong to the Charopidae (J. H. Hartman, pers. comm. 1996).

Paleoecology

Among the mammals, the species diversity and abundance of small lipotyphlan insectivores is remarkable, even when the assemblage is compared with other Clarkforkian micromammal assemblages such as University of Michigan locality SC-188 in the Clark’s Fork Basin (Krause, 1986) (Table 4.3; Fig. 4.5). By far the most common species is a hedgehog belonging to the genus *Leipsanolestes*. Eleven species of basal primatomorphs (early relatives of primates and flying lemurs) are known from Big Multi Quarry. This is an extraordinarily high species richness for this group at a single site, but their combined abundance is comparable to that at other Clarkforkian and late Tiffanian localities (Fig. 4.5). Only one species of marsupial occurs*, Peradectes protinnominatus*, but this species is exceptionally abundant in comparison to total marsupial abundance at sites of roughly similar age in the Rocky Mountain region (Fig. 4.5). Multituberculates are reasonably abundant and diverse (four species), whereas this group is unknown from the early Clarkforkian Bear Creek fauna of southern Montana. Interestingly, the relative abundance of multituberculates in two of the best-sampled Clarkforkian mammal assemblages (Big Multi Quarry and SC-188) is similar to or greater than that from an assemblage that antedates the dispersal of rodents into North America (Princeton Quarry, from late Tiffanian zone Ti5; Fig. 4.5). This finding conflicts with the notion that the immigration of rodents severely affected North American multituberculates (Krause, 1986). In contrast to the primarily surface-collected Clarkforkian sites in the Clark's Fork Basin, large mammal taxa are not disproportionately represented at Big Multi Quarry, although some large-bodied forms are present. These include the uintathere *Probathyopsis*, the pantodont *Cyriacotherium*, the condylarths *Phenacodus* and *Ectocion*, and the carnivoran *Didymictis*. Diversity indices indicate greater mammalian faunal heterogeneity and evenness than for primarily surface-collected Clarkforkian assemblages from the Clark's Fork Basin (Table 4.4).

For the plants, both frequencies of occurrence (Table 4.2) and census results (Table 4.5) demonstrate the overwhelming dominance of *Corylites* leaves both in the near-channel environment found above Big Multi Quarry (USNM loc. 41263) and in the backswamps preserved at the 18-m level. *Corylites* was found at 11 of the 15 localities and constituted 1065 of the 1564 leaves in the four censuses combined. It was common at the plant localities from the 18-m level to find 20-30 *Corylites* leaves in a single block and no other species, a possible result of synchronous abscission of leaves (i.e., deciduousness). The fact that all extant Betulaceae are deciduous supports this hypothesis. However, even if deciduousness exaggerated the leaf counts in favor of *Corylites*, the lopsidedness of the census results leaves no doubt that the tree bearing *Corylites* leaves and *Palaeocarpinus aspinosa* fruits (Manchester and Chen, 1996) dominated the areas nearest to depositional centers.

The only challenges to *Corylites* dominance were the strong showings of *"Ampelopsis*" *acerifolia* at USNM loc. 41270 and of "*Cinnamomum*" *sezannense* above Big Multi Quarry. However, *Glyptostrobus europaeus*, although not censused, occurred at the greatest number of localities (Table 4.2). From qualitative observations, *G. europaeus* foliage was clearly not as abundant as *Corylites* but was nevertheless very common. *Persites argutus* was also ubiquitous, occurring at ten localities, but it was not a dominant element in any of the censuses. Similarly, aff. Cercidiphyllaceae occurred at seven localities but at very low abundance.

The overall dominance pattern is very similar to that described by Gemmill and Johnson (1997) for the Tiffanian Bison Basin plant assemblage. There, the two leading rank dominants are *Corylites* sp., also in association with *Palaeocarpinus aspinosa*, and *Archeampelos acerifolia* (probably the same species as our "*Ampelopsis*" *acerifolia*), while the third is *Metasequoia occidentalis*, a taxodiaceous conifer that may have occupied a niche similar to *Glyptostrobus europaeus*. However, at our sites, *Corylites* is even more dominant in the leaf counts, comprising 68.1% of total dicot leaves vs. 49.3% in the Bison Basin.

Diversity indices are shown for the censused quarries in Table 4.5. The site immediately above Big Multi Quarry, USNM loc. 41263, has the second highest values. Diversity indices from ten Tiffanian quarries in the Bison Basin are comparable although slightly higher (Simpson: cumulative 0.559, mean 0.484; Shannon: cumulative 1.02, mean 0.880; Gemmill and Johnson, 1997, Appendix 1, adjusted for dicots only). The greater percentage of *Corylites* leaves at our sites is a primary cause of the lower index values at our sites than in the Bison Basin. The low values of diversity indices in both the Bison Basin and Big Multi assemblages could reflect the biological and preservational limitations on species richness and evenness that can be recovered from individual fossil plant localities of floodplain environments (Wing and DiMichele, 1995). However, these index values are well below those from early Eocene assemblages from similar depositional settings in the nearby Great Divide Basin, strongly supporting the argument for originally low evenness in the late Paleocene (Wilf, unpublished data).

Low-diversity forests are typical of the early and middle Paleocene worldwide (e.g., Crane et al., 1990; Wing and Sues, 1992), and in western North America, these conditions have been documented as late as the Tiffanian (Hickey, 1980; Gemmill and Johnson, 1997). The monotony of Paleocene forests stands in sharp contrast to the contemporaneous radiation of mammals (Wing and Fleming, 1995; Alroy, 1996). Our data show that even in the Clarkforkian, during a period of warming associated with the immigration of exotic mammals and plants, the overall structure of basin forests remained monotonous in southern Wyoming, not to be reorganized until the early Eocene (Wilf, unpublished data).

Biostratigraphic Correlation

Assignment of the Big Multi Quarry mammalian assemblage to the Clarkforkian NALMA is secure, based on the occurrence of both rodents and tillodonts in the fauna (Rose, 1980, 1981a; Archibald et al., 1987). In the Clark’s Fork Basin, finer biostratigraphic zonation of the Clarkforkian is based on species of plesiadapids that have not been adequately documented at Big Multi Quarry. However, many of the mammals occurring at Big Multi Quarry imply correlation with the early part of the Clarkforkian NALMA, and correlation with zone Cf1 is advocated here. For example, the multituberculate *Microcosmodon conus* and the plagiomenid *Planetetherium* have never been found in strata as young as middle Clarkforkian (Cf2) in the Clark's Fork Basin, suggesting an earlier age for Big Multi Quarry. Taxa that seemingly corroborate this age assignment include (1) *Carpolestes nigridens*; (2) a species of *Chiromyoides* that is smaller and more primitive than *C. major*; and (3) a species of *Aletodon* that is similar to and possibly conspecific with *A. conardae* (late Tiffanian) but smaller and more primitive than *A. gunnelli* (middle and late Clarkforkian). On the other hand, it seems unlikely that Big Multi Quarry is as old as the Bear Creek, Montana, mammalian assemblage, the best sampled early Clarkforkian fauna available for comparison, because *Leipsanolestes* n. sp. from Big Multi Quarry is more derived than *L. siegfriedti* from Bear Creek in having a more nearly molariform P_4. On the basis of the entire mammalian assemblage, we correlate Big Multi Quarry with early, but not earliest Clarkforkian strata in the Clark's Fork Basin. Big Multi Quarry thus antedates the latest Paleocene thermal maximum, which is considered to be synchronous with the Clarkforkian/Wasatchian boundary (Kennett and Stott, 1991; Koch et al. 1992; Thomas and Shackleton, 1996).

The plant assemblage (Table 4.2) is completely consistent with published megafloral zonations for the Clarkforkian of the Bighorn Basin (Hickey, 1980; Wing, 1998). That is, all of the Big Multi plants also found in the Bighorn Basin are found in Clarkforkian strata in the Bighorn Basin, as shown in Table 4.2. The only exception, *Woodwardia gravida*, is known from the Clarkforkian of North Dakota (Hickey, 1977).

This result is encouraging for careful application and further development of megafloral zonations tied to NALMAs.

At a finer scale, the local plant assemblage more closely resembles middle Clarkforkian and later floras of the Bighorn Basin, which, given the early Clarkforkian age determined from the fauna, suggests northward floral migration coincident with climatic warming. The *Persites-Cornus* Zone (PCZ; Hickey, 1980), named for the conjunction of *Persites argutus* and *Cornus hyperborea*, has been correlated to Clarkforkian and earliest Wasatchian strata in the Bighorn Basin (Hickey, 1980; Wing, 1998). Recently, the PCZ has been divided into lower and upper parts (Wing, 1998), with an approximate boundary between the parts within Cf2 time. Using this zonation, the Big Multi plant assemblage clearly falls into the upper part because two diagnostic characteristics of the upper PCZ are: (1) *Corylites* sp. is dominant at many localities and co-occurs with its presumed fruits, *Palaeocarpinus aspinosa* (Manchester and Chen, 1996), as in our assemblage (Tables 4.2, 4.5); (2) three taxa that are characteristically abundant in the lower PCZ are uncommon or extinct in the upper PCZ. Two are definitely not present in our study area: "*Viburnum*" *asperum* Newberry, and "*Viburnum*" *cupanioides* (Newberry) Brown. The third, "*Viburnum*" *antiquum* (Newberry) Hollick appears to be absent, although the morphotype FW40 is possibly a variant form of this taxon (Table 4.2). All three "Viburnums" have long pre-Clarkforkian Paleocene ranges throughout the Rocky Mountains and Great Plains (Brown, 1962; Hickey, 1980), including the Fort Union Formation of the Rock Springs Uplift (Brown, 1962; Gemmill and Johnson, 1997; Wilf, unpublished data).

Given the conflict between an early Clarkforkian faunal age and floral composition similar to middle and late Clarkforkian floras of northern Wyoming, elements and abundance patterns of the local plant assemblage appear to be diachronous with those in northern Wyoming. This hypothesis needs to be tested with further study, but it is strongly supported by recent work in the Tiffanian of the nearby Great Divide Basin, where *Corylites* sp. is also overwhelmingly dominant and also co-occurs with *Palaeocarpinus aspinosa* (Manchester and Chen, 1996; Gemmill and Johnson, 1997). In addition, *P. aspinosa* is only known from the Fort Union Formation of the Greater Green River and Bighorn basins of Wyoming, despite an extensive survey of Paleocene sites in the Rocky Mountains and Great Plains that yield *Palaeocarpinus* spp. by Manchester and Chen (1996). Therefore, the absence of *P. aspinosa* in the Tiffanian and early Clarkforkian of the Bighorn Basin is probably not a local biogeographic peculiarity of the Bighorn Basin among other basins north of our study area. This absence also seems very unlikely to be an artifact of undersampling in the Bighorn Basin, where the megaflora has been heavily sampled and temporal hiatuses are rare throughout this time interval (Hickey, 1980; Wing et al., 1995). Finally, it is highly improbable that the lack of a pattern as obvious as *Corylites* dominance could be due to undersampling.

We suggest that the *P. aspinosa* tree, which dominated southern Wyoming floodplain forests in the Tiffanian and early Clarkforkian, spread to northern Wyoming in the early Clarkforkian, presumably in response to climatic warming, and dominated forests there in the middle and late Clarkforkian. This northward range extension of native flora stands in contrast to the more rapid and contemporaneous southward migration of exotic mammals and possibly plants that dispersed across high-latitude land bridges. Warming was also detrimental to long-lived taxa that were poorly adapted to these conditions. For example, the three “Viburnums” suffered decreases in abundance and then extinction, apparently in the warmer south before the cooler north.

PALEOENVIRONMENTAL AND PALEOCLIMATIC RECONSTRUCTION

Sedimentology and Depositional Environments

We interpret the coarsening-up sequences in our section (Fig. 4.3) as sequential overbank events associated with avulsion cycles of the local fluvial system. Each sequence records the increasing proximity of river channels and their subsequent avulsions onto low-lying, distal swamps. The swamps are represented by the carbonaceous shales and coals that occur at the bases of the sequences. Adjacent, vegetated areas of slight relief are represented by the rooted underclays. During coal and carbonaceous shale formation, distal areas were starved of sediment because of their distance from the main fluvial channels and the rarity of flood events capable of transporting sediment far out onto the floodplain. As channels migrated and relocated nearer to formerly distal areas, increasingly coarser grained and greater amounts of sediment were deposited there during flood events. This deposition is represented by the siltstones and fine sandstones of the middle parts of coarsening-up sequences. Finally, when channels avulsed onto the lower parts of the floodplain, cross-bedded sandstones were deposited, which are observed at the upper part of coarsening-up sequences. This system is similar to that described by Davies-Vollum (1996) and Davies-Vollum and Wing (1998) for deposits in the Bighorn Basin.

The lack of red beds and the predominantly drab colors of lithologies in the section indicate deposition under low-oxygen, probably waterlogged conditions that kept iron compounds in their reduced, gray-green colored state (e.g., Wilding and Rehage, 1985; Retallack, 1991). The orange coloration at the 1-m level is clearly secondary because it occurs preferentially at plant fossil layers and is due to infiltration of waters into the porous sandstone and redeposition of iron minerals. Natrojarosite, the yellow mineral that stains coal and carbonaceous shales, is secondary, occurring after pyrite (Bouma et al., 1990). Pyrite forms in slightly acidic, reduced conditions, and is also associated with waterlogging (Chague-Goff et al., 1996). The thin, featureless paleosols that occur as underclays below carbonaceous shales and coals are interpreted as periodically dry, hydromorphic soils of vegetated swamps that became permanently waterlogged at the onset of carbonaceous shale deposition (Atkinson, 1986; Davies-Vollum, 1996), similar to the wettest of the “simple paleosols” described by Kraus and Aslan (1993) from the Willwood Formation of the Bighorn Basin.

The presence of muscovite-rich sandstones is consistent with the interpretation of Kirschbaum et al. (1994) of south to southeast-flowing drainage on a nearly flat Paleocene floodplain. The drainage system flowed from the ancestral, crystalline Wind River Mountains to the north, the source for the muscovite. Volcanic activity is indicated by a laterally extensive, highly degraded ash deposit of unknown source near the base of the carbonaceous shale at the 18-m level (Fig. 4.3).

Although fossil plants and vertebrates are found in close stratigraphic proximity, they are not found in the same bed in any part of the section. This suggests that the two different kinds of fossils were preferentially preserved by different environmental or depositional conditions. The fossil mammal-bearing bed has a purple color, often associated with wet, oxygenated paleosols (Bown and Kraus, 1981). Oxidizing environments tend to degrade plant material and preclude fossilization. Conversely, the acidic conditions often associated with the reduced, swampy environments where plant fossils are typically preserved tend to destroy bone material before it can be fossilized. The two preservational regimes indicate variation in substrate chemistry, probably associated with changes in waterlogging that can be attributed to position on the floodplain relative to the main channel system.

Total organic carbon content for beds bearing vertebrates and plants varies between 3.8-8.6% (Table 4.1). Coarser-grained samples tend to have lower TOC, but higher TOC is not required for good preservation; many whole leaves came from the sandstone at the 1-m level, which has the lowest TOC studied, 3.8%. Influxes of relatively coarse sediment can “sandwich” layers of organic material, inhibiting the accumulation of organic mats but facilitating the preservation of individual, identifiable leaf fossils.

The drab color of all lithologies in our section, the dark color of coals, the hydromorphic nature of the paleosols, and the absence of redbeds, differentiated soil horizons, and carbonate nodules all strongly indicate conditions that were moist year-round, without major seasonal variation in substrate moisture content and precipitation. Formation of paleosol carbonate nodules generally requires a moisture deficit, and the absence of such nodules implies soil saturation and a water table that was near the substrate surface with little seasonal fluctuation (Arkley, 1963; Sobecki and Wilding, 1982). Rooting in the underbeds, however, suggests that conditions were not so waterlogged as to inhibit plant colonization and growth. As the major topographic lows in the area at this time were further south, along the ancient Uinta Mountain Front (Kirschbaum et al. 1994), the coals in our section are not primarily tectonic but represent humid conditions.

Nearest Living Relatives and Functional Analogues

The presence of salamanders, turtles, a champsosaur, and alligatorid crocodilians at Big Multi Quarry implies relatively moist environmental conditions. The large-bodied and presumably piscivorous champsosaurs are consistent with fairly large bodies of standing water and/or medium-to-large streams and rivers (Bartels, 1983). This possibility is reinforced by the presence of the pantolestid mammal *Palaeosinopa*. Pantolestids have long been considered to have been semi-aquatic and otter-like in their adaptations (Matthew, 1909), a view that is strongly corroborated by functional analyses and fossilized gut contents of the middle Eocene European pantolestid *Buxolestes piscator* (Koenigswald, 1980; Pfretzschner, 1993). The occurrence of two species of alligatorids reflects warm and equable climatic conditions, "with coldest-month mean temperatures of >7°C, mean annual temperatures of >16°C, and mean annual temperature ranges of <21.1°C" (Markwick, 1994, p. 616).

The high species richness of basal Primatomorpha suggests the presence of forested, or at least woodland, conditions because most or all of these taxa were highly arboreal, and several of them show adaptations for gliding (Beard, 1990, 1991, 1993b). Other mammalian taxa that were likely to have been at least partly arboreal include the marsupial *Peradectes* (Szalay, 1994), the apatemyid *Labidolemur* (Koenigswald and Schierning, 1987), the arctocyonid condylarth *Chriacus* (Rose, 1987), and the rodent *Paramys* (Szalay, 1985).

The presence of palms and gingers strongly suggests frost-free conditions (e.g., Greenwood and Wing, 1995). All extant gingers are tropical, about 1300 species (Heywood, 1993). Palms are a widespread group of about 2800 species characterized, with only a handful of exceptions, by a profound physiological incapacity to withstand hard freezes (Sakai and Larcher, 1987; Heywood, 1993; Doughty et al., 1994; Greenwood and Wing, 1995). According to Greenwood and Wing (1995), palms are restricted to “climates with mean annual temperature > 10°C, cold month mean temperature > 5°C, and yearly minimum temperature > -10°C”.

The nearest living relatives of some of the fossil plants are strongly associated with continuously wet conditions, and none indicate dry environments. The most significant in this regard are the ferns and horsetails. These plants are characteristically found in moist areas because their life cycles include both free-living haploid generations, which are usually highly vulnerable to drying, and aqueous fertilization. Recent experimental work on horsetail spores has shown that their viability is irreparably compromised after only two weeks of desiccation (Lebkuecher, 1997). *Glyptostrobus* is probably another good indicator of damp to waterlogged environments, although its past distribution far exceeded its present range and could have once included better-drained environments (e.g., Wolfe, 1980).

Cenogram Analysis

A cenogram for Big Multi Quarry is presented in Figure 4.6. Alternative cenograms were constructed using different regression models for particular taxa, but these did not substantially affect paleoenvironmental interpretation. The slope of the least squares regression line through the cenogram points corresponding to medium-sized mammals (0.5-10 kg) has been related to environmental moisture, with many mammal species occupying the medium-size category (yielding lower slopes) in humid environments and fewer species occupying this size category (yielding higher slopes) in drier environments (Legendre, 1989; Gingerich, 1989; Gunnell, 1994, 1997; Gunnell and Bartels, 1994). The value obtained for this parameter for Big Multi Quarry is near the mean for modern faunas characterized as occurring in “subhumid” forests and savannas (Fig. 4.7A). Among other North American Paleocene assemblages, similar values for medium mammal slope have been documented at another Clarkforkian locality, SC-188 in the Clark's Fork Basin (Cf2), and at the Torrejonian Rock Bench Quarry, Bighorn Basin, by Gunnell (1994). In contrast, cenograms for Tiffanian localities analyzed by Gunnell (1994) uniformly yielded higher values for the medium mammal slope, suggesting drier conditions in the Tiffanian than in either the Torrejonian or the Clarkforkian.

The vertical offset between small and medium-sized mammals on a cenogram has been related to vegetational structure (Legendre, 1989; Gingerich, 1989; Gunnell, 1994, 1997; Gunnell and Bartels, 1994). Many species traverse the gap separating small from medium-sized mammals in closed, forested settings, yielding smaller values for the vertical offset, while fewer species occupy this size range in more open vegetational settings, yielding higher values. Uniquely among North American Paleocene mammal assemblages analyzed to date, the cenogram for Big Multi Quarry shows a very small vertical offset, corresponding to closed forest conditions among modern mammal faunas (Fig. 4.7B). In contrast, cenograms for all other Paleocene mammal assemblages, including the Cf2 locality SC-188, yield much higher values for the vertical offset (Gunnell, 1994). These values correspond to more open, woodland and/or savanna vegetational settings among modern faunas. Although Big Multi Quarry may actually sample a more closed, forested environment than do these other Paleocene mammal assemblages, we believe that an alternative possibility must also be considered: that the latter assemblages are relatively incomplete samples of the faunas from which they were derived. If this is the case, their vertical offsets are likely to be spuriously exaggerated in favor of "open" conditions. This line of reasoning is supported in the case of SC-188 by the previously discussed similarity in floral composition between the Big Multi plant assemblage and Cf2 floras of the Bighorn Basin.

Leaf Margin and Area Analysis

Leaf-margin analysis indicates mean annual temperatures approaching 20°C (Table 4.6). In comparison to the Bighorn Basin, this is warmer than leaf-margin temperatures near 13°C in Cf1 time and 16°C for Cf2 and Cf3 time (Wing et al., 1999). This result is consistent with the more southerly location and also matches our floristic data that show late Clarkforkian floral elements of northern Wyoming to be present in southern Wyoming in the early Clarkforkian and before, suggesting that both a warmer climate and a thermophilic flora invaded northern Wyoming from the south during the Clarkforkian. Mean annual temperatures near 20°C, even in today's highly seasonal climate, are associated with winter temperatures far above freezing. Seasonal variation in temperature must have been present in the study area due to changes in light regime at middle latitudes, which may have been responsible for the inferred deciduous habit of some of the plants. However, frosts were rare and brief. Leaf-area analysis of the Big Multi plant assemblage yields estimated mean annual precipitation near 137 cm (Table 4.6).

Climatic Summary

The multiple lines of evidence presented above as well as Roehler's (1979) original paleoclimatic assessment are mutually consistent. The study area was a humid, subtropical, forested floodplain without significant frost or marked moisture deficits. Considerable emphasis has been placed on the exceptionally warm global conditions of the terminal Paleocene and early Eocene and on the enigma of warm continental interiors in the early Eocene (e.g., Sloan, 1994; Greenwood and Wing, 1995). Our data add to this enigma by documenting humid subtropical conditions in a continental area before the latest Paleocene thermal maximum. A plausible hypothesis for future study is that the climate of southern Wyoming was influenced by oceanic warmth that arrived via water vapor, possibly from a persistent Cannonball Sea (see Smith et al., 1994: Map 9).

ECOSYSTEM SYNTHESIS

The diverse fauna found at Big Multi Quarry lived on a humid subtropical floodplain with little relief, on which meandering streams and rivers flowed south across a flattened Rock Springs Uplift, carrying clay and muscovitic sand from the ancestral Wind River Mountains towards the Uinta Mountain Front and the Mississippi Embayment. Distal areas of the floodplain were occupied by sinking peat swamps, adjacent to periodically dry, forested soils. These swamps were filled in by overbank deposits from successive flood events as the main channel migrated closer, at first depositing clays and later increasing grain sizes until the channel itself occupied the site of the former swamp and deposited cross-bedded sand. The channel then migrated, allowing peat deposition at the start of a new fluvial cycle. The floodplain forest was frequently disturbed by this channel activity.

A single species of the birch family that presumably bore *Corylites* leaves and *Palaeocarpinus aspinosa* fruits was overwhelmingly dominant in all environments. *Glyptostrobus europaeus* was also common. The laurel family was well represented, and *"Ampelopsis" acerifolia*, *Cornus hyperborea*, and a cercidiphylloid dicot filled out much of the inferred phytomass. *Averrhoites affinis* and *"Cinnamomum" sezannense* were abundant in near-channel environments, while a variety of dicots as well as ferns and horsetails lived in the swampiest areas. Forest structure was homogeneous in comparison both to modern subtropical forests and to early Eocene forests in Wyoming (Davies-Vollum and Wing, 1998; Wilf, unpublished data).

These forested conditions supported a variety of arboreally adapted mammals. Taxonomically dominant among these were archaic relatives of living primates and flying lemurs, although squirrel-like rodents (*Paramys adamus*) and small arboreal marsupials (*Peradectes protinnominatus*) were also abundant. A species of hedgehog (*Leipsanolestes* n. sp.) was by far the most common mammal, although numerous additional species of tiny-to-small lipotyphlan insectivores occupied the forest floor. Mammalian herbivores of small-to-large size included hyopsodontid and phenacodontid condylarths, a tillodont, a pantodont, and a uintathere. The mammal assemblage also included an armadillo-like species (*Palaeanodon* sp., cf. *P. parvulus*), an otter-like form (*Palaeosinopa*), two species of carnivorans, and four species of multituberculates. Additional biota in the area included reptiles, amphibians, insects, and pulmonate gastropods.

CONCLUSIONS

Big Multi Quarry is the most diverse fossil vertebrate locality yet known from the Clarkforkian Land Mammal Age. The mammalian fauna can be correlated with early, but not earliest, Clarkforkian faunas of the Bighorn Basin, about 350 km to the north. The closely associated flora includes nearly all of the fossil plant species known from coeval rocks in the region. Floristic composition and abundance patterns better match middle and late than early Clarkforkian floras of northern Wyoming, supporting a scenario of northward floral migration in step with the overall Clarkforkian warming trend. The well-exposed local section has also yielded reptiles, amphibians, gastropods, and insect feeding traces. These fossil organisms represent a forested floodplain ecosystem in a humid subtropical climate that existed before the latest Paleocene thermal maximum. Mean annual temperature was near 20°C and mean annual precipitation near 137 cm, with limited or no seasonal frost or marked dry season. Such warm and moist conditions are associated in the early Eocene and today with moderately high plant species richness, mixed dominance, and spatial heterogeneity. However, plant communities in our study area were not species-rich, were strongly dominated by a single species, and were spatially homogeneous. These ecological conditions were typical of the cooler earlier Paleocene. Thus, the “temperate” ecology of Paleocene basin forests made its last stand in the area in the Clarkforkian as the earth warmed, mammalian diversity increased, and thermophilic plant taxa arrived. This scenario may have implications for understanding the resistance of modern temperate forests to perturbation by global warming.

Reconstructions of ancient environments are greatly strengthened by considering as wide a variety of evidence as possible. The uncertainties involved in the application of any single method are substantial, and analysis based on a preponderance of evidence from more than one methodology, applied at more than one spatial scale, greatly reduces the probability of incorrect conclusions and broadens interpretation.

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TABLE 4.1—Total organic carbon content (TOC) for selected beds.

TABLE 4.2—Floral list, with presence-absence data and previously known range in the Tiffanian to Lostcabinian of the Bighorn Basin (from Wing, 1998). *f* = frequency. Ranges: Ti, Tiffanian; Cf1-3, Clarkforkian Zones 1-3; GB, Graybullian; LC, Lostcabinian. Organs: A, axis; F, foliage; C, cone; Ca, calyx; Fr, fruit. “sl” = found at same stratigraphic level as the quarry, usually within 20 m, but not at the quarry itself.

TABLE 4.3—Mammalian faunal composition at Big Multi Quarry. For purposes of cenogram analysis, the natural logarithm of body mass was calculated from measurements of lower first molar area in each species, according to regression equations published by Legendre (1989). See text for discussion regarding estimates of body mass in multituberculates and palaeanodonts.

TABLE 4.4—Diversity indices for Paleocene and early Eocene mammalian assemblages from the western United States. Comparative data for localities other than Big Multi Quarry are from Gunnell (1994) and references therein. Diversity indices as in Rose (1981a).

TABLE 4.5—Dicot leaf census data: raw leaf counts and diversity indices (formulae in Table 4.4).

TABLE 4.6—Leaf-margin and leaf-area data. T, toothed margin; E, entire margin; Na, Nanophyll; Mi, Microphyll; No, Notophyll; Me, Mesophyll; Ma, Macrophyll (Webb, 1959).

TABLE 4.1

Sample	Meter level	Lithology / fossils	%TOC
USNM loc. 41272	18	fissile siltstone / plants	5.5
USNM loc. 41272	18	fissile siltstone / plants	5.8
USNM loc. 41272	18	carbonaceous shale-siltstone / plants	7.6
USNM loc. 41269	18	carbonaceous shale / plants	7.8
USNM loc. 41269	18	lignite	84
USNM loc. 41275-76	11	mudstone / plants	5.8
USNM loc. 41264	4	sandstone / plants	5.2
USNM loc. 41263	1	sandstone / plants	3.8
Big Multi Quarry	0.5	mudstone / vertebrates	5.8
Big Multi Quarry	0.5	organic mudstone / vertebrates	8.6
Big Multi Quarry	<0.5	gray mudrock / vertebrates	6.2

TABLE 4.2

		USNM locality number 412- (meter level)															
	Organ	62 (1)	63 (1)	64 (4)	75 (11)	76 (11)	65 (18)	66 (18)	67 (18)	68 (18)	69 (18)	70 (18)	71 (18)	72 (18)	73 (18)	74 (18)	Frequency	Range
Sphenopsida																		
Equisetum sp.	A	_	_	_	_	_	_	_	_	_	_	_	_	_	_	x	1	Cf1-LC
Polypodiopsida																		
BLECHNACEAE																		
Woodwardia gravida Hickey	F	_	_	_	_	_	_	_	_	x	_	x	_	x	_	_	3	GB-LC
?POLYPODIACEAE																		
Allantodiopsis erosa Lesquereux	F	_	_	_	_	_	_	_	_	_	_	_	x	x	x	x	4	Cf1-LC
Pinopsida																		
TAXODIACEAE																		
Glyptostrobus europaeus (Brogniart) Heer	F, C	x	x	x	_	_	x	_	x	x	x	x	x	x	x	x	12	Ti-LC
Metasequoia occidentalis Newberry	F, C	_	_	_	_	_	x	_	_	_	_	_	_	_	_	_	1	Ti-GB
Liliopsida																		
ARECACEAE																		
Amesoneuron sp. Goeppert	F	_	_	_	_	_	_	_	x	_	_	_	_	x	_	_	2	Cf1-LC
ZINGIBERACEAE																		
Zingiberopsis isonervosa Hickey	F	_	_	x	_	_	_	x	_	_	_	_	_	_	_	_	2	Cf1-LC
Magnoliopsida																		
BETULACEAE																		
Corylites sp. Gardner	F	x	x	_	_	_	x	x	x	x	x	x	_	x	x	x	11	Cf1-GB
Palaeocarpinus aspinosa Manchester and Chen	Fr	x	x	_	_	_	x	_	x	x	x	x	_	_	_	x	8	Cf2-3
?CERCIDIPHYLLACEAE																		
aff. Cercidiphyllaceae FW09	F	x	x	_	_	_	_	_	x	_	x	_	_	x	sl	x	6	
CORNACEAE																		
Cornus hyperborea Heer	F	_	x	_	_	_	_	_	_	_	_	x	_	x	_	x	4	Cf1-GB
JUGLANDACEAE																		
"Carya" antiquorum Newberry	F	_	_	_	_	_	_	_	_	_	_	x	_	_	_	_	1	Ti-GB
LAURACEAE																		
"Cinnamomum" sezannense Watelet	F	x	x	_	_	_	_	_	_	_	_	_	_	_	_	_	2	Cf1-Cf3
aff. *Ocotea* FW03	F	_	_	_	_	_	_	_	x	x	_	x	_	x	x	x	6	
Persites argutus Hickey	F	x	x	_	x	x	_	x	x	_	_	x	x	x	_	x	10	Cf1-GB
?LAURACEAE																		
"Ficus" planicostata Lesquereux	F	x	_	_	_	_	_	_	_	_	_	_	_	_	_	_	1	Cf2-GB
MAGNOLIACEAE																		

TABLE 4.2

		USNM locality number 412- (meter level)																
	Organ	62 (1)	63 (1)	64 (4)	75 (11)	76 (11)	65 (18)	66 (18)	67 (18)	68 (18)	69 (18)	70 (18)	71 (18)	72 (18)	73 (18)	74 (18)	Frequency	Range
Magnoliaceae sp. FW07-22-46	F	_	_	_	_	_	_	_	x	_	_	x	_	_	_	x	3	
MYRTACEAE																		
Palaeomyrtinaea sp. Pigg, Stockey, and Maxwell	Fr	_	_	_	_	_	_	_	_	_	_	x	_	_	_	_	1	
?PLATANACEAE																		
"Ficus postartocarpoides" FW06	F	_	_	_	_	_	_	_	_	_	x	x	_	_	_	x	3	Cf1-3
?VITACEAE																		
“Ampelopsis” acerifolia (Newberry) Brown	F	_	_	_	_	_	x	x	x	x	_	x	x	_	x	x	8	Ti-GB
INCERTAE SEDIS																		
Averrhoites affinis (Newberry) Hickey	F	_	_	x	_	_	sl	_	_	_	_	x	_	x	_	_	3	Cf1-LC
Calycites sp. FW13	Ca	_	_	x	_	_	_	_	_	_	_	_	_	_	_	_	1	
aff. “*Viburnum*” *antiquum* Hollick FW40	F	_	_	_	_	_	_	_	_	_	_	x	_	_	_	x	2	
FW05	F	_	_	_	_	_	_	_	_	_	x	_	_	_	_	_	1	
FW18	F	_	_	_	_	_	_	_	x	_	_	_	_	x	_	_	2	
FW23	F	_	_	_	_	_	_	_	_	_	x	_	_	_	_	_	1	
FW24	F	_	_	_	_	_	_	_	_	_	_	_	_	_	_	x	1	
FW25	F	_	_	_	_	_	x	_	_	_	_	_	_	_	_	_	1	
FW27	F	_	x	_	_	_	_	_	_	_	_	_	_	_	_	_	1	
FW31 ?aquatic herb	F	_	_	_	_	_	_	_	_	x	_	_	_	_	_	_	1	
?herbaceous rosette of ?leaves FW58	F	_	_	_	_	_	_	_	_	_	_	x	_	_	_	_	1	
fertile catkin FW65	Fr	_	_	x	_	_	_	_	_	_	_	_	_	_	_	_	1	
FW68	F	_	_	_	_	_	_	_	_	_	_	_	_	_	_	x	1	
SITE RICHNESS (nonreproductive)		6	7	3	1	1	5	4	9	6	6	12	4	11	5	14		

Notes. “aff.” = strong morphological similarity. Quotation marks = assignment thought to be invalid. Morphotype numbers (FW) shown for undescribed forms. *Woodwardia gravida* material is sterile; assignment based on fertile material found in nearby Clarkforkian rocks in the Sand Butte Rim NW Quadrangle (Wilf, unpublished data). “*Ficus postartocarpoides*” = “*F.*” *artocarpoides*, *sensu* Wing (1998). The modified name is used to separate the morphotype from nomenclatural issues involving “*F.*” *artocarpoides* Lesquereux and “*F.*” *preartocarpoides* Brown (see Johnson, 1996). FW40 is consistently narrower and less cordate than “*Viburnum*” *antiquum* as usually defined but shares other architectural features. Figured descriptions and additional references for the species designated with author names can be found in Brown (1962), Hickey (1977), Pigg et al. (1993), and Manchester and Chen (1996).

TABLE 4.3

Taxon	TNS/MNI	%TNS	%MNI	ln (M_1area, mm^2)	ln (body mass, g)	Regression model
Multituberculata						
Microcosmodon conus	70/13	4.19	4.98	0.24	2.66	All Mammal
Neoliotomus conventus	3/1	0.18	0.38	2.45	6.42	All Mammal
Ectypodus powelli	124/16	7.42	6.13	-0.057	2.15	All Mammal
Parectypodus laytoni	4/3	0.24	1.15	-0.39	1.59	All Mammal
Marsupialia						
Peradectes protinnominatus	175/21	10.47	8.05	0.24	3.24	Marsupial
Lipotyphla						
Palaeoryctes sp., cf. *P. punctatus*	12/3	0.72	1.15	0.96	3.08	Refined Insectivore
Leipsanolestes n. sp.	340/48	20.33	18.39	1.23	3.59	Refined Insectivore
Plagioctenodon sp. A	73/16	4.37	6.13	0.12	1.53	Refined Insectivore
Plagioctenodon sp. B	81/12	4.84	4.60	0.78	2.76	Refined Insectivore
Wyonycteris sp.	93/14	5.56	5.36	0.32	1.90	Refined Insectivore
Limaconyssus sp.	26/6	1.56	2.30	0.73	2.67	Refined Insectivore
Ceutholestes sp.	13/3	0.78	1.15	0.73	2.66	Refined Insectivore
cf. *Mckennatherium*, n. gen., n. sp.	5/2	0.30	0.77	0.74	2.68	Refined Insectivore
Diacocherus minutus	2/1	0.12	0.38	1.01	3.18	Refined Insectivore
Placentalia, incertae sedis						
Labidolemur kayi	13/2	0.78	0.77	0.74	2.68	Refined Insectivore
Palaeosinopa sp.	7/1	0.42	0.38	2.45	6.43	All Mammal
Planetetherium n. sp.	13/2	0.78	0.77	2.07	5.77	All Mammal
Primatomorpha						
Chiromyoides n. sp.	11/3	0.66	1.15	1.99	6.13	Primate
Plesiadapis dubius	3/1	0.18	0.38	1.95	6.07	Primate
Plesiadapidae, large sp.	2/1	0.12	0.38	3.37	8.50	Primate
Carpolestes nigridens	88/11	5.26	4.21	0.89	4.23	Primate
Phenacolemur simonsi	37/4	2.21	1.53	0.74	4.01	Primate
Phenacolemur pagei	41/4	2.45	1.53	1.56	5.41	Primate
cf. *Ignacius*, n. gen., n. sp.	21/6	1.26	2.30	2.07	6.27	Primate
Arctodontomys simplicidens	18/4	1.08	1.53	1.95	6.07	Primate
Arctodontomys n. sp.	19/5	1.14	1.92	0.80	4.10	Primate
Tinimomys n. sp.	38/7	2.27	2.68	-0.13	2.51	Primate
Chalicomomys n. sp.	5/1	0.30	0.38	-0.11	2.56	Primate
“Condylarthra”						
Phenacodus intermedius	8/1	0.48	0.38	4.75	10.80	Ungulate
Ectocion osbornianus	27/4	1.61	1.53	3.74	9.27	Ungulate
Apheliscus nitidus	114/11	6.82	4.21	1.84	5.39	All Mammal

Taxon	TNS/MNI	%TNS	%MNI	ln (M_1area, mm^2)	ln (body mass, g)	Regression model
Aletodon sp., cf. *A. conardae*	5/1	0.30	0.38	2.74	6.92	All Mammal
Chriacus sp.	6/1	0.36	0.38	3.32	7.91	All Mammal
Dinocerata						
Probathyopsis sp., cf. *P. harrisorum*	2/1	0.12	0.38	5.00	10.78	All Mammal
Pantodonta						
Cyriacotherium psamminum	1/1	0.06	0.38	3.54	8.28	All Mammal
Tillodontia						
Azygonyx xenicus	2/1	0.12	0.38	3.81	8.74	All Mammal
Rodentia						
Paramys adamus	94/13	5.62	4.98	0.79	3.48	Refined Rodent
Alagomys russelli	58/10	3.47	3.83	-0.31	1.54	Refined Rodent
Palaeanodonta						
Palaeanodon sp., cf. *P. parvulus*	1/1	0.06	0.38		6.62	All Mammal
Carnivora						
Viverravus sp.	8/2	0.48	0.77			
Didymictis sp.	9/3	0.54	1.15			
Total	1672/261					

TABLE 4.4

Locality/Zone	Simpson (D)	Shannon (H')	Whittaker (E)
Rock Bench Quarry (To3)	0.954	3.40	33.3
Douglass Quarry (Ti1)	0.952	3.40	35.2
Scarritt Quarry (Ti2)	0.811	2.03	11.2
Cedar Point Quarry (Ti3)	0.877	2.64	18.1
Chappo Type Locality (Ti3)	0.904	2.77	16.6
Princeton Quarry (Ti5)	0.937	2.97	24.6
Clarkforkian Zone Cf1	0.865	2.59	17.5
Big Multi Quarry	**0.937**	**3.13**	**24.3**
Clarkforkian Zone Cf2	0.866	2.62	16.6
Clarkforkian Zone Cf3	0.878	2.62	17.1
Wasatchian Zone Wa0	0.940	3.20	31.9
Wasatchian Zone Wa1	0.925	2.85	24.1
Wasatchian Zone Wa2	0.921	2.90	21.6
Wasatchian Zone Wa3	0.928	2.89	21.4

Simpson Index (D) = $1 - \sum [n_i (n_i - 1)]/[N(N-1)]$, where
n_i = number of individuals in species i
N = total number of individuals in sample

Shannon Index (H') = $- \sum p_i (\ln p_i)$, where
p_i = proportion of the i^{th} species

Whittaker Index (E) = $s/(\log p_1 - \log p_s)$, where
s = number of species
p_1 = proportion of individuals in the most common species
p_s = proportion of individuals in the rarest species

TABLE 4.5

	USNM locality no. 412-				
	63	65	70	72	Total
“Ampelopsis” acerifolia	0	6	269	11	286
“*Cinnamomum*” *sezannense*	109	0	0	0	109
aff. Cercidiphyllaceae	7	0	0	0	7
Cornus hyperborea	0	0	13	0	13
Corylites sp.	180	274	284	327	1065
Magnoliaceae sp.	0	0	19	0	19
aff. *Ocotea*	0	0	12	22	34
Persites argutus	2	0	22	3	27
aff. “*Viburnum*” *antiquum*	0	0	2	0	2
FW18	0	0	0	1	1
FW25	0	1	0	0	1
#Specimens	298	281	621	364	1564
Simpson (mean 0.336)	0.502	0.049	0.602	0.189	0.498
Shannon (mean 0.620)	0.794	0.127	1.13	0.427	1.052

TABLE 4.6

Taxon	Margin	Area
“*Ampelopsis*” *acerifolia*	T	Mi-Me
Averrhoites affinis	E	Mi-Me
"*Carya*" *antiquorum*	T	Mi-No
aff. Cercidiphyllaceae	T	Mi-No
"*Cinnamomum*" *sezannense*	E	Mi-Me
Cornus hyperborea	E	Mi-Me
Corylites sp.	T	Mi-Me
"*Ficus postartocarpoides”*	T	Mi-No
"*Ficus*" *planicostata*	E	Me
Magnoliaceae sp.	E	Mi-Ma
aff. *Ocotea*	E	Mi-Me
Persites argutus	E	Na-Me
aff. “*Viburnum*” *antiquum*	T	Mi-No
FW 05	T	No
FW 18	T	Mi-Mi
FW 23	E	Mi
FW 24	E	Mi
FW 25	E	Mi-Me
FW 27	E	No-Me
FW 68	E	Mi

Proportion entire margins	0.600
MAT estimate, °C	19.5 ± 3.35
MlnA	7.58
MAP estimate, cm	137 +59.2, - 41.4

Notes. MAT estimate from leaf-margin analysis (Wolfe, 1979; Wing and Greenwood, 1993); error shown is binomial sampling error, which is a minimum error of the estimate (Wilf, 1997). MlnA = mean natural log of the species’ leaf-areas (Wilf et al., 1998); MAP estimate from leaf-area analysis (Wilf et al., 1998); error bars of one standard regression error are asymmetrical because they were converted from logarithmic units.

FIGURE 4.1—The Greater Green River Basin of southwestern Wyoming, redrawn after Roehler (1992), showing major subbasins and uplifts (gray). Big Multi Quarry is located in the northwestern Washakie Basin, near Bitter Creek (starred).

FIGURE 4.2—Big Multi Quarry. The shovel rests on the vertebrate-bearing mudstone (V), above which is a thin lignite (L) and a horizon bearing abundant fossil plants (P).

FIGURE 4.3—Measured section and expanded sections through Big Multi Quarry and plant bearing beds. The lower expanded section is through Big Multi Quarry (Fig. 4.2); the upper is adjacent to the most diverse fossil plant localities, USNM locs. 41270 and 41274, which are not on the main line of section.

FIGURE 4.4— Relative abundance of mammals in three different size classes at Big Multi Quarry and a modern woodland assemblage from the Ohio River valley. Body size for the fossil mammal species was estimated using regressions of body size versus M_1 area in extant mammalian groups (see Table 4.3 and text). The distribution of body size in the extant woodland sample is adapted from Gunnell (1994) and references therein. Size categories are as follows: I, less than 0.5 kg; II, 0.5 kg-10 kg; III, greater than 10 kg.

FIGURE 4.5—Relative abundance of major groups of mammals at Big Multi Quarry and penecontemporaneous localities in the northern Bighorn Basin, based on minimum number of individuals (MNI). Comparative data for Bighorn Basin localities are derived from Rose (1981a) and Krause (1986).

FIGURE 4.6—A cenogram for Big Multi Quarry. The gray area indicates the size range for medium-sized mammals, 500 g to 10 kg. Vertical offset is calculated about the lower dashed horizontal line. Body weight data from Table 4.3. Slope of least squares

regression line through data points for medium sized mammals is 0.35; vertical offset between data points on either side of the 0.5 kg threshold is 0.14.

FIGURE 4.7—Paleoenvironmental results of cenogram analysis. (A) Variation in slope of the least squares regression line through cenogram data points for medium-sized mammals in Big Multi Quarry and selected fossil and extant faunas. This cenogram parameter is related to environmental moisture in extant mammal faunas. (B) Variation in values for the vertical offset between cenogram data points on either side of the 0.5-kg threshold in Big Multi Quarry and selected fossil and extant faunas. This cenogram parameter is related to vegetational regime in extant mammal faunas. Values for fossil faunas other than Big Multi Quarry are derived from Gunnell (1994); values for extant mammal faunas are derived from Gunnell and Bartels (1994), and references therein.

FIGURE 4.1

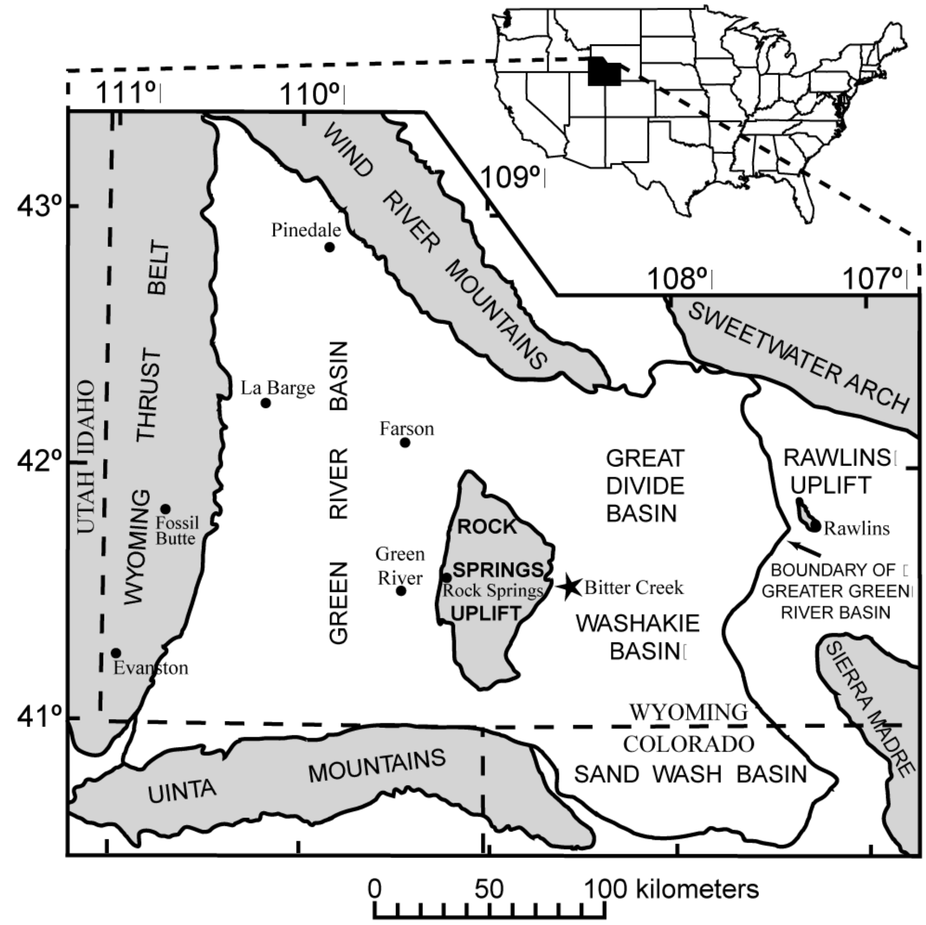

111°
110°
109°
108°
107°
43°
42°
41°
WIND RIVER MOUNTAINS
WYOMING THRUST BELT
UTAH
IDAHO
Pinedale
La Barge
Farson
GREEN RIVER BASIN
Fossil Butte
Evanston
Green River
ROCK SPRINGS UPLIFT
Rock Springs
Bitter Creek
GREAT DIVIDE BASIN
WASHAKIE BASIN
SWEETWATER ARCH
RAWLINS UPLIFT
Rawlins
BOUNDARY OF GREATER GREEN RIVER BASIN
SIERRA MADRE
WYOMING
COLORADO
SAND WASH BASIN
UINTA MOUNTAINS
0
50
100 kilometers

FIGURE 4.2

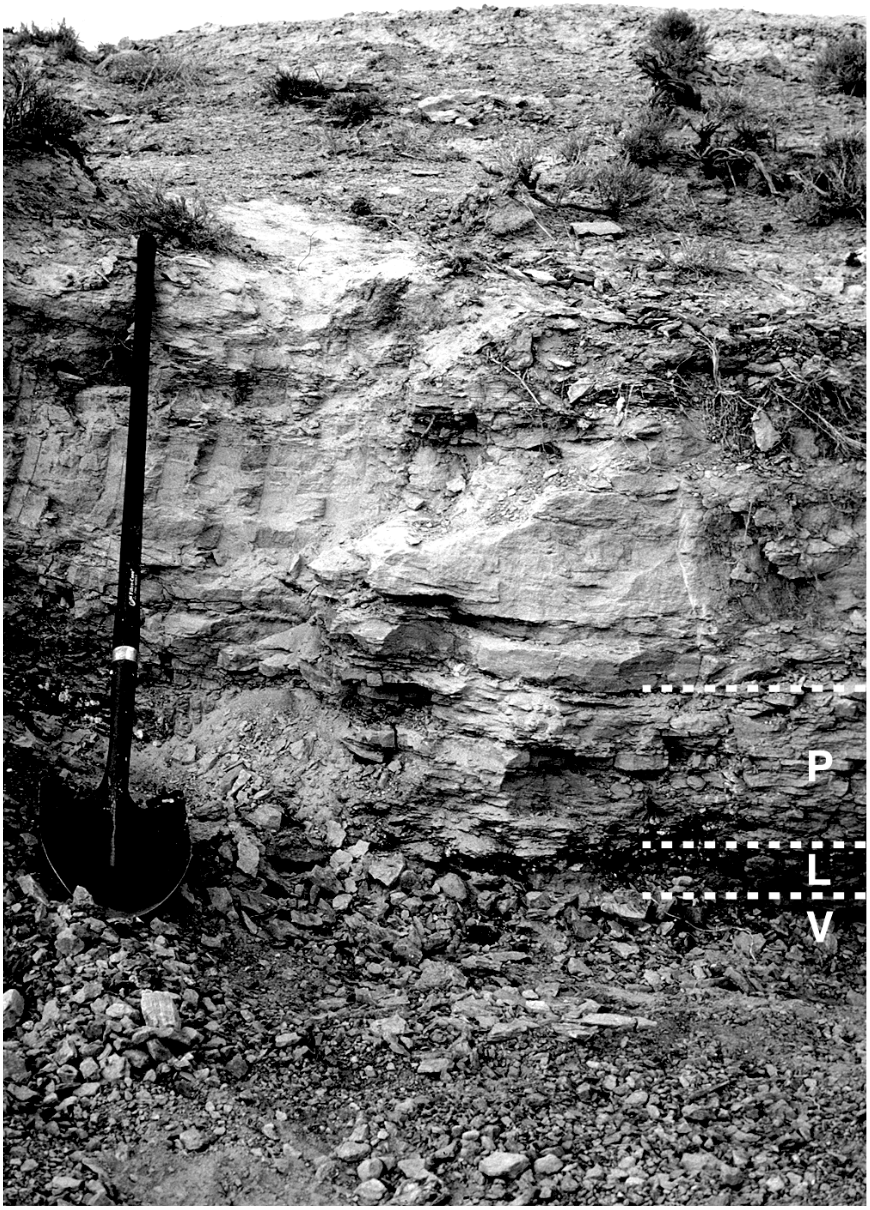
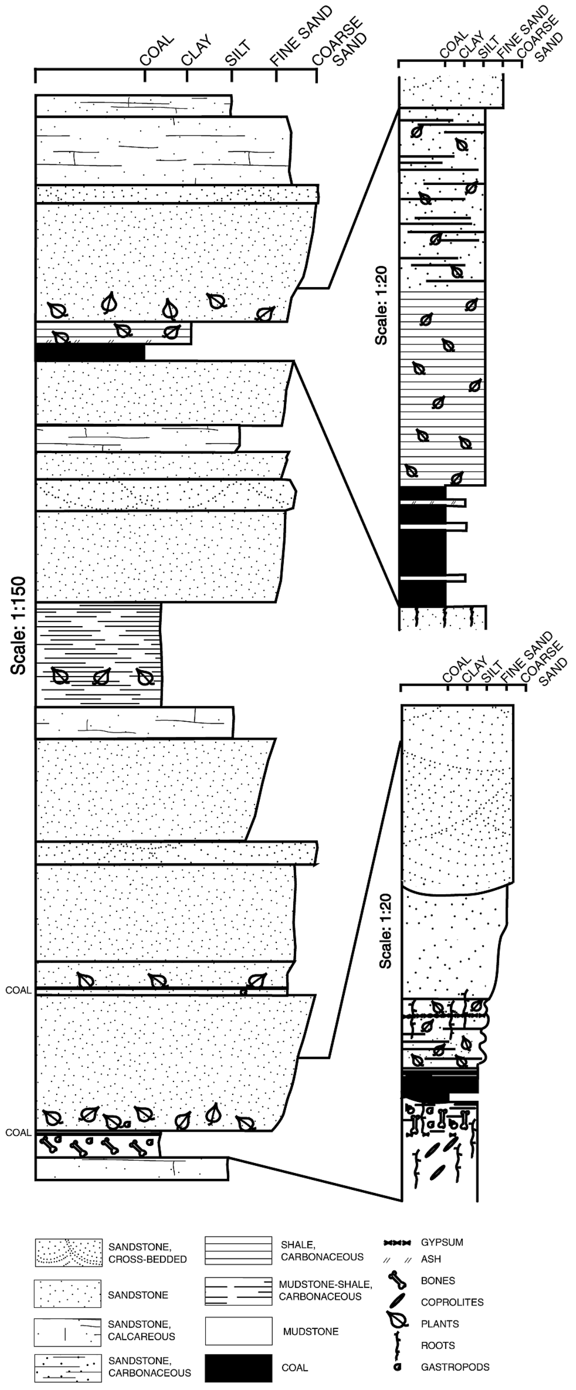
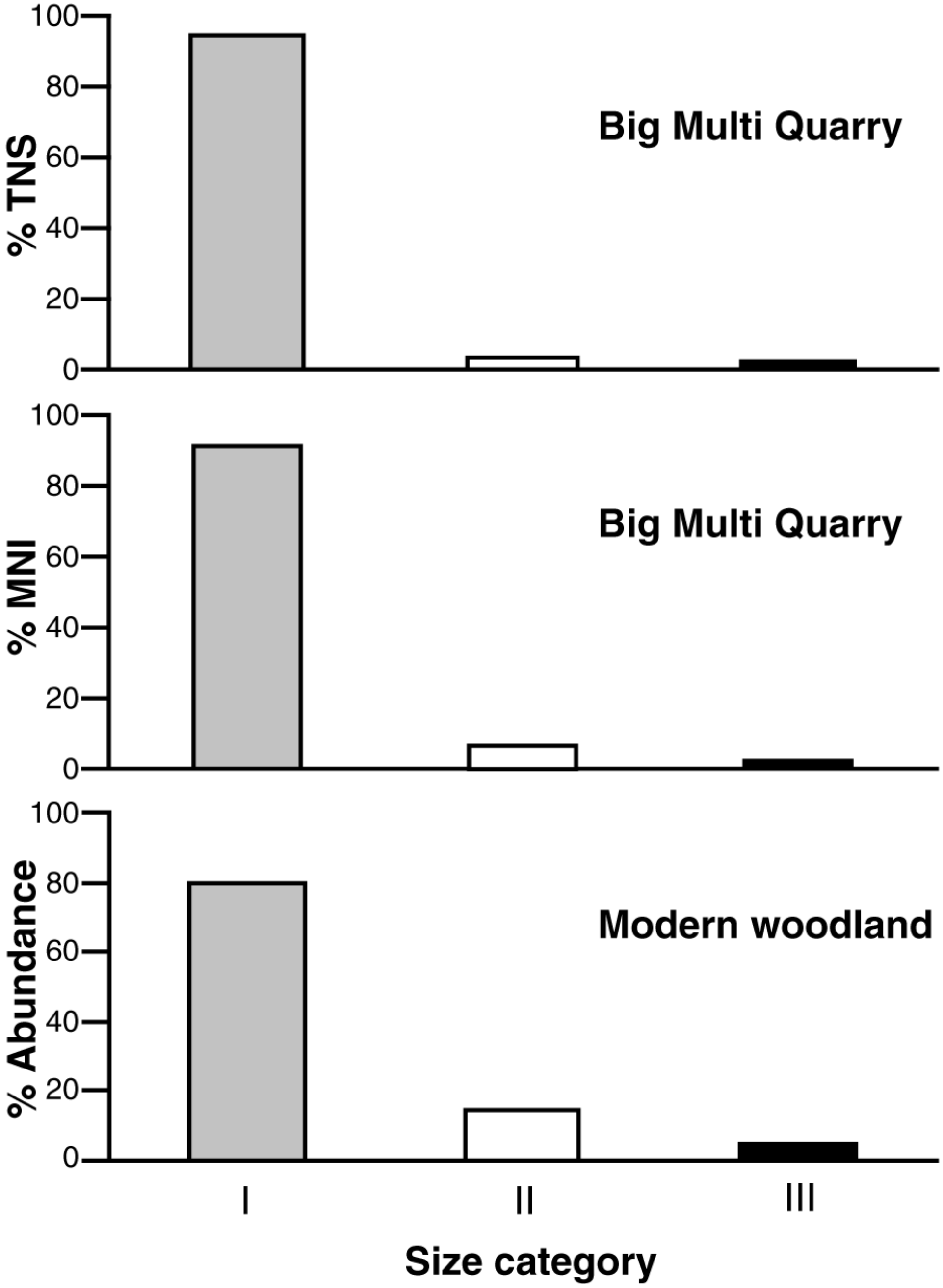


FIGURE 4.3


COAL
CLAY
SILT
FINE SAND
COARSE SAND
Scale: 1:150
Scale: 1:20
Scale: 1:20
COAL
COAL
SANDSTONE, CROSS-BEDDED
SANDSTONE
SANDSTONE, CALCAREOUS
SANDSTONE, CARBONACEOUS
SHALE, CARBONACEOUS
MUDSTONE-SHALE, CARBONACEOUS
MUDSTONE
COAL
GYPSUM
ASH
BONES
COPROLITES
PLANTS
ROOTS
GASTROPODS


% TNS
Big Multi Quarry
% MNI
Big Multi Quarry
% Abundance
Modern woodland
0
20
40
60
80
100
I
II
III
Size category

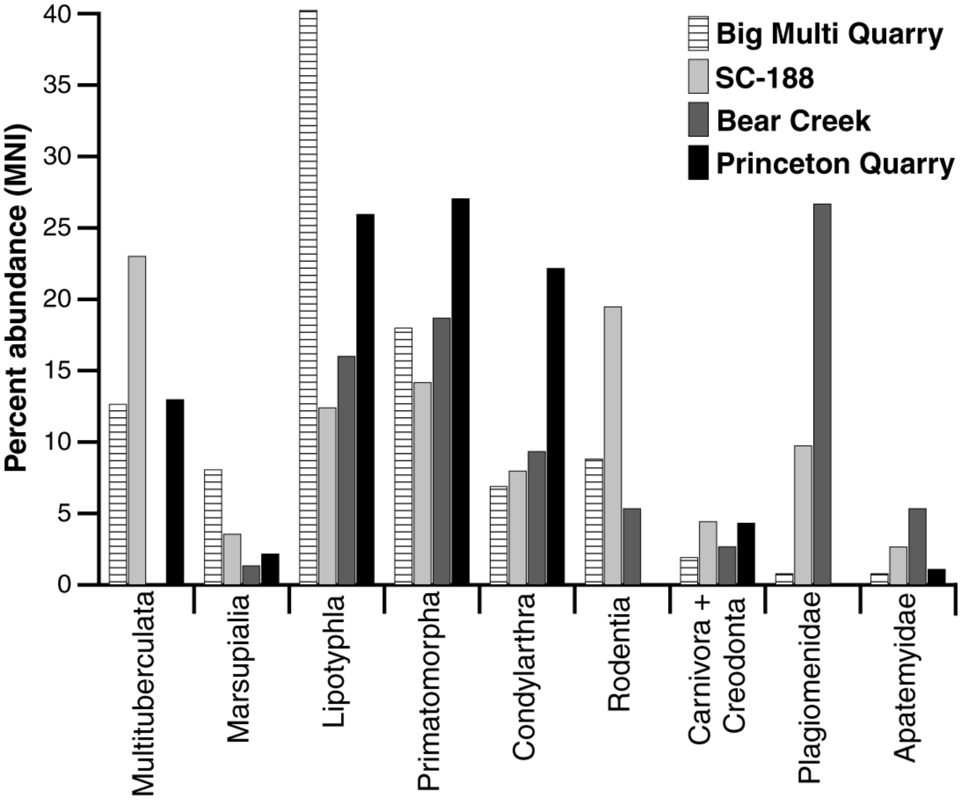
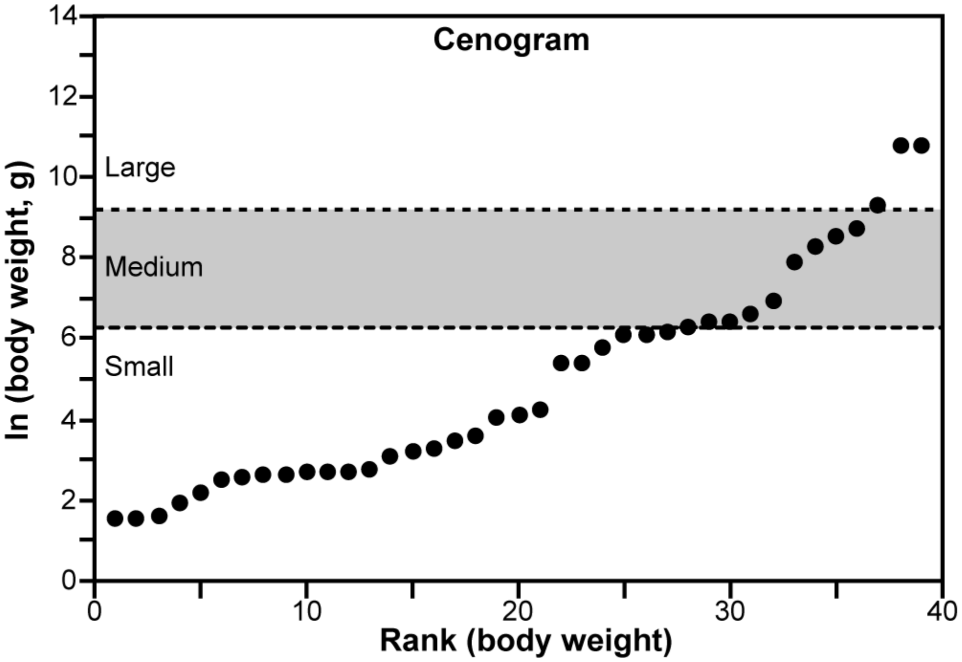
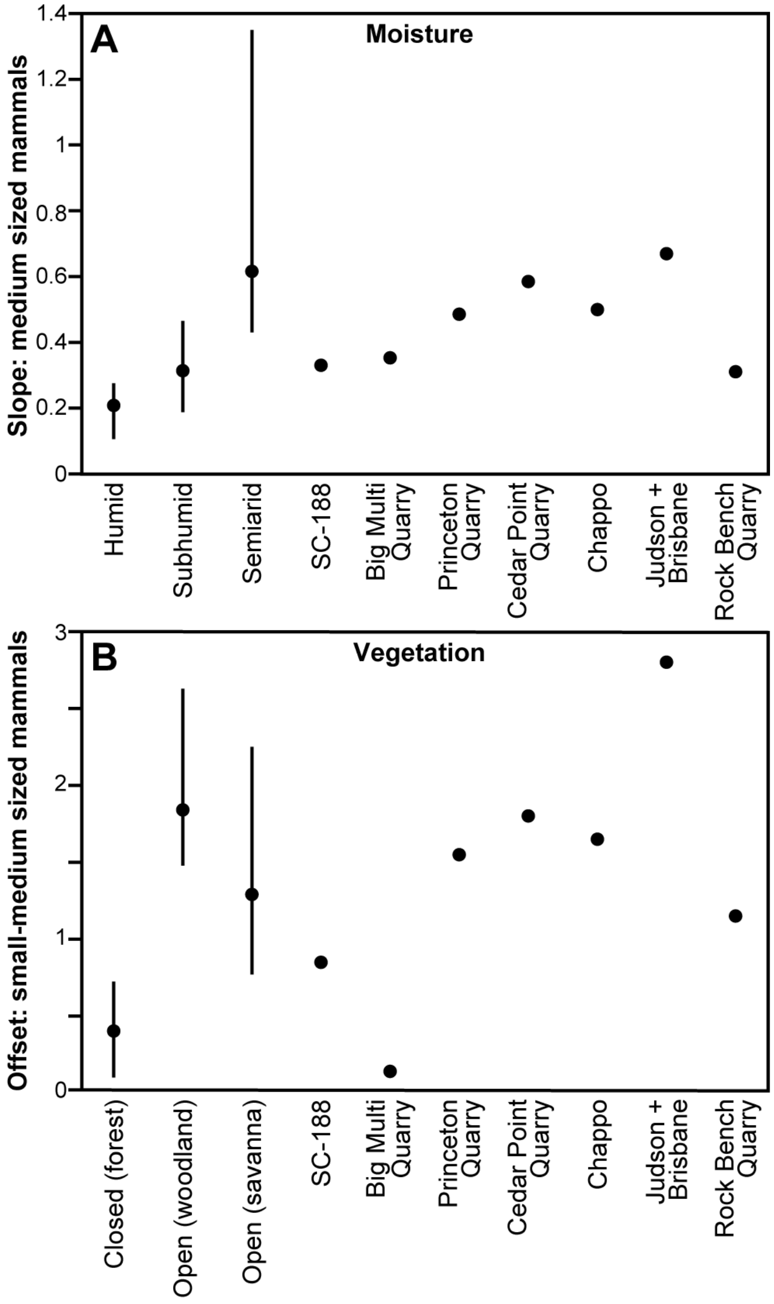

Percent abundance (MNI)
0
5
10
15
20
25
30
35
40
Big Multi Quarry
SC-188
Bear Creek
Princeton Quarry
Multituberculata
Marsupialia
Lipotyphla
Primatomorpha
Condylarthra
Rodentia
Carnivora + Creodonta
Plagiomenidae
Apatemyidae

FIGURE 4.6


Cenogram
Large
Medium
Small
ln (body weight, g)
Rank (body weight)
0
2
4
6
8
10
12
14
0
10
20
30
40


A
Moisture
Slope: medium sized mammals
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Humid
Subhumid
Semiarid
SC-188
Big Multi Quarry
Princeton Quarry
Cedar Point Quarry
Chappo
Judson + Brisbane
Rock Bench Quarry
B
Vegetation
Offset: small-medium sized mammals
3
2
1
0
Closed (forest)
Open (woodland)
Open (savanna)
SC-188
Big Multi Quarry
Princeton Quarry
Cedar Point Quarry
Chappo
Judson + Brisbane
Rock Bench Quarry

CHAPTER FIVE

PALEOBOTANICAL ANALYSIS OF LATE PALEOCENE-EARLY EOCENE CLIMATE CHANGES IN THE GREATER GREEN RIVER BASIN OF SOUTHWESTERN WYOMING

This chapter is written in the style of the journal *Geological Society of America Bulletin*, where it has been submitted for publication.

Paleobotanical analysis of late Paleocene-early Eocene climate changes in the Greater Green River Basin of southwestern Wyoming

Peter Wilf *Department of Paleobiology, MRC 121, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560*

ABSTRACT

The warmest global temperatures of the Cenozoic occurred in the early Eocene, following a warming trend that started in the late Paleocene. The Greater Green River Basin of southwestern Wyoming is one of the best areas in the Rocky Mountains for paleobotanical investigation of the Paleocene-Eocene climatic transition. Intensive sampling has resulted in the recovery of an estimated 146 species of plant macrofossils from the Clarkforkian, Wasatchian, and Bridgerian Land Mammal Ages. The Clarkforkian environment was humid and subtropical, following cooler humid conditions in the Tiffanian, and many plant families with modern tropical affinities immigrated into southern Wyoming. However, as in the Tiffanian, Clarkforkian fossil vegetation had low diversity and was overwhelmingly dominated by a single species in the birch family. Mean annual temperature (MAT) rose from about 13°C in the Tiffanian to nearly 20°C in the Clarkforkian, and estimated mean annual precipitation (MAP) in the Clarkforkian was near 150 cm. Very little fossil plant material is preserved from the latest Clarkforkian or earliest Wasatchian. By the middle Wasatchian, the time of the Cenozoic thermal maximum, MAT was about 22°C, and MAP was again near 150

cm after a possibly cooler and drier interval. A second wave of modern tropical families immigrated into the area and diversity increased, but most plant families known from the Clarkforkian persisted. Species turnover from the Clarkforkian to the Wasatchian was over 80%. A second major turnover of species (but not families) in the early Bridgerian accompanied severe drying and increased seasonality of precipitation. The Bridgerian fossil vegetation consisted of subtropical scrub growing next to an expanded phase of a cyclical playa lake system; MAT was near 19°C and MAP about 75 cm. Except for the Tiffanian and possibly portions of the Graybullian, the entire study interval was predominantly frost-free. The moderating influence of the Green River lake system has been suggested as a possible explanation for mild Eocene winters in Wyoming. This study shows that mild climates existed in the area prior to significant lake development.

INTRODUCTION

The geologic record provides the only documentation of the effects of long-term global climate change. Certainly one of the most instructive past time periods for understanding the processes and results of global warming was the early Eocene, the warmest time period of the Cenozoic, which followed a warming trend that started in the late Paleocene (Corfield and Cartlidge, 1992; Zachos et al., 1994; Wing et al., 1995). Some of the classic examples of global warmth at this time are alligators and flying lemurs on Ellesmere Island (Dawson et al., 1976), Southern Beech forests in Antarctica (Case, 1988), and kaolinite deposition off of Antarctica (Robert and Chamley, 1991;

Robert and Kennett, 1992). This time period is especially useful for potential insight into the effects of warming because its biota was phylogenetically closer to the modern biota than that of previous warm intervals in the Cretaceous. Several climate modeling studies have investigated the early Eocene (e.g., Sloan and Barron, 1992; Sloan, 1994; Sloan and Rea, 1995; Bice et al., 1997). These simulations have tended to generate freezing winters in continental interior areas thought by paleontologists to have been predominantly frost-free (Sloan and Barron, 1992; Sloan, 1994; Greenwood and Wing, 1995).

Most of what is known about the Paleocene-Eocene transition on a fine temporal scale comes from marine cores (Kennett and Stott, 1991; Thomas and Shackleton, 1996; Bralower et al., 1997). Nearly all fine-scale continental data, especially paleobotanical data, are derived from a single area, the Bighorn Basin of northwestern Wyoming (Hickey, 1980; Wing and Bown, 1985; Wing et al., 1991, 1999; Bown et al., 1994; Wing, 1998). The relative lack of data from elsewhere, even from other areas in the Rocky Mountains (Hickey, 1977), makes it difficult to place events observed in the Bighorn Basin into a global or even regional context.

Plant macrofossils in the Greater Green River Basin of southwestern Wyoming (Fig. 5.1) are well preserved and diverse through most of the Paleocene-Eocene interval, and a combination of mammalian biostratigraphy, radiometric dating, and extensive previous lithostratigraphic work provides an excellent stratigraphic context. This area is also the subject of a recent climate modeling study by Sloan (1994), which examined the possibility that the Green River lake system, which existed in the area for about 8 my starting in the middle early Eocene, had an ameliorating effect on Wyoming climate. Abundant fossil plants are preserved from Paleocene and Eocene sediments below the first lake deposits, providing data to assess whether warm and frost-free conditions existed independent of lake effects.

This paper, the first major paleobotanical field study of the Paleocene-Eocene transition in this region, investigates the following questions: (1) what climatic changes occurred in this area in the late Paleocene and early Eocene?; (2) how did the ancient vegetation respond to these changes in terms of composition, turnover, and diversity?; (3) did warm and frost-free conditions exist independent of the Green River lakes?; and (4) how do the patterns of climatic and floristic change compare with those known from the Bighorn Basin?

SETTING

The Greater Green River Basin (Fig. 5.1) comprises most of southwestern Wyoming and contains exposed continental rocks of Campanian through middle Eocene (Uintan) age in a large number of subbasins. Today this area is high desert, with less than 30 cm of annual rainfall, January mean temperature near -10°C, and only about 100 frost-free days (Knight, 1994). Late Paleocene and early Eocene time is primarily represented by the fluvial Paleocene Fort Union Formation, the fluvial early Eocene Wasatch Formation, and the predominantly lacustrine early and middle Eocene Green River Formation, which interfingers with the Wasatch Formation (Fig. 5.2). The majority of the plant fossils recovered for this study were found in the Fort Union Formation of the Washakie and Green River Basins, the Wasatch Formation of the central and eastern Great Divide Basin, and the Green River Formation of the Green River Basin (Figs. 5.1, 5.2; Appendix 5.1).

PREVIOUS WORK

A prolific literature has existed on all aspects of the geology of the Greater Green River Basin for nearly a century and a half (e.g., Leidy, 1856; Hayden, 1871). Broad summaries can be found in Roehler (1992c, 1993). I note here only previous investigations that are most relevant to this study. The current stratigraphic framework for the region has been established largely through four decades of geologic mapping by H. W. Roehler (Roehler, 1992a, 1992b, 1992c). In addition to his many published reports, Roehler archived bed-by-bed lithologic descriptions of all of his sections at the Wyoming Geological Survey, Laramie. This resource was consulted extensively for this investigation. Other lithostratigraphic work used here includes mapping of the early Eocene coal fields of the Great Divide Basin by Pipiringos (1961) and Masursky (1962), in the central and eastern portions of the basin, respectively, and a measured section in the Dry Canyon area of the Green River Basin (Kirschbaum, 1987; Kirschbaum and Nelson, 1988).

Vertebrate paleontology provides an invaluable biochronologic framework for the area through the well established system of North American Land Mammal Ages (NALMAs) (Wood et al., 1941; Woodburne, 1987). Faunal turnover events marking the NALMA boundaries have repeatedly been shown to be virtually isochronous throughout North America (Flynn et al., 1984, 1989; Alroy, 1998). Mammalian fossils have been collected in or near the study area by many investigators, so the NALMA system is useful here (Morris, 1954; Gazin, 1956, 1962, 1965; McKenna, 1960; Pipiringos, 1961; West, 1973; West and Dawson, 1973; Roehler, 1977, 1979, 1992b; Savage and Waters, 1978; Rose, 1981a; Winterfeld, 1982; Honey, 1988; Williams and Covert, 1994; Dawson and Beard, 1996; Anemone et al., 1996; Clyde et al., 1997; Wilf et al., in press).

The relationship of NALMAs relevant to this paper to the conventional time scale is shown in Figure 5.2. In addition to these investigations, substantial unpublished, stratigraphically controlled collections of fossil vertebrates from the area are housed at the University of California Museum of Paleontology.

Paleobotanical literature from the study area is historically sparse, although this situation has improved somewhat in recent years. Palynological data have been published for the upper Fort Union Formation (Tschudy in Roehler, 1979), a Fort Union-Wasatch section in the Dry Canyon area of the Green River Basin (Kirschbaum, 1987), the Eocene Washakie Basin reference section (Leopold in Roehler, 1992b), and the Niland Tongue of the Wasatch Formation in the Vermilion Creek Basin (Nichols, 1987).

A series of systematic papers on plant macrofossils has shed light on the phylogenetic affinities of some of the regional paleoflora. The Juglandaceae have a long record in the area, which has been treated in several studies (MacGinitie, 1969; Manchester and Dilcher, 1982, 1997; Wing and Hickey, 1984; Manchester, 1987). This record includes the oldest juglandaceous species currently recognized, *Polyptera manningii*, known primarily from the (?early) Tiffanian of the Rock Springs Uplift (Manchester and Dilcher, 1997). The betulaceous fruit *Palaeocarpinus aspinosa*, in association with *Corylites* sp. leaves, is ubiquitous in most upper Paleocene rocks of the area and was described by Manchester and Chen (1996). In his monograph of the Green River flora of Colorado and Utah, MacGinitie (1969) provided a preliminary floral list for the Bridgerian Little Mountain flora of the uppermost Wilkins Peak Member of the Green River Formation in the Green River Basin. Herendeen and others have described *Ceratophyllum muricatum*, a living species, and a fossil species of *Caesalpinia* subgenus *Mezoneuron* in part from Little Mountain material (Herendeen et al., 1990;

Herendeen and Dilcher, 1991). Manchester and Zavada (1987) described attached leaves and sporophores of *Lygodium kaulfussi*, a long-ranging Eocene species, from the Bridger Formation northwest of Rock Springs.

Two recent paleoecological studies of the upper Fort Union Formation have improved our knowledge of vegetation, paleoecology and paleoclimate in the late Paleocene in the area and are incorporated into this article. Gemmill and Johnson (1997) studied plant paleoecology and provided a floral list from ten quarries along strike of a single bed from the Tiffanian of the Bison Basin, a subbasin of the northern Great Divide Basin. Wilf et al. (in press) published a floral and faunal list and a paleoecological and paleoclimatic study based on fossil plants, vertebrates, and sediments of the 18 m section immediately associated with early Clarkforkian Big Multi Quarry (Fig. 5.1).

Several previous analyses of paleoenvironments and paleoclimate are available. Roehler (1979) interpreted the upper Fort Union Formation of the northwestern Washakie Basin as the deposits of a humid subtropical floodplain. Wilf et al. (in press) strongly supported this conclusion in their study of the Big Multi local section, finding diverse evidence from fauna, flora, and lithologies for mean annual temperatures near 19.5°C and mean annual precipitation near 137 cm, with no evidence for either freezing winters or a marked dry season. Kirschbaum et al. (1994) demonstrated that late Paleocene paleocurrents in the vicinity of the Rock Springs Uplift were predominantly southerly, flowing from the ancestral Wind River Mountains, across a Rock Springs Uplift flattened by erosion, to join north-flowing streams in front of the Uinta Mountains with subsequent drainage to the east.

Grande (1994) demonstrated subtropical to tropical conditions in the Lostcabinian of southern Wyoming based on the fauna of the Fossil Butte Member of the Green River

Formation in the area of Fossil Butte (Fig. 5.1), which includes reptiles with strong tropical affinities such as crocodiles, alligators, tropical wood snakes (Tropidopheidae), and varanid lizards, and fishes of the Osteoglossidae, Gonorynchidae, and Pellonulinae, all known today only from the tropics. Nichols (1987), on the basis of palynological analysis of the Lostcabinian Niland Tongue in the Vermilion Creek Basin, concluded that climate was subtropical, without freezing temperatures, and that rainfall was probably “abundant”.

Several sedimentological and floristic papers have addressed the depositional environment and climate of the Wilkins Peak Member of the Green River Formation, in which the Little Mountain assemblage is found (Bradley, 1964; MacGinitie, 1969; Leopold and MacGinitie, 1972; Eugster and Hardie, 1975; Surdam and Wolfbauer, 1975; Smoot, 1983; Roehler, 1993). The sedimentological studies point to cyclically evaporitic conditions in a playa-lake system bordered by mud flats, responsible for the deposition of the world’s largest known reserves of trona. Presumably, high surrounding uplifts at this time created rain shadows that contributed to these dry conditions (see Norris et al., 1996). The Little Mountain assemblage most likely is derived from forest that grew at a highstand of the lake, on the wettest portions of alluvial fans, surrounded by forested surrounding slopes (Eugster and Hardie, 1975; Smoot, 1983; Wing, 1987). MacGinitie (1969) and Leopold and MacGinitie (1972) considered the Little Mountain assemblage to represent a dry, subtropical environment on the basis of floristic affinities to modern seasonally dry tropical forests and a high abundance of small, coriaceous leaves. The discovery of fossil flamingos in intertonguing fluvial sediments corroborated this interpretation (McGrew, 1971). Herendeen et al. (1990) noted the restriction of living *Ceratophyllum muricatum* to subtropical and tropical climates. *Caesalpinia* subgenus

Mezoneuron is restricted to the modern paleotropics (Herendeen and Dilcher, 1991). Wing and Greenwood (1993) published climatic estimates based on analyses of leaf physiognomy for the entire Green River flora, of which the Little Mountain assemblage is one of the oldest components, of 14-15°C mean annual temperature and 116 cm mean annual precipitation. The latter was subsequently revised to 84 cm by Wilf et al. (1998).

Roehler (1993) produced the most recent detailed overview of Eocene paleoenvironments and paleoclimates in the area, based primarily on lithologies and plant fossils then available. His climatic summary was that "early Eocene climate was warm temperate to subtropical; the late early and early middle Eocene climate was cyclically hot arid and warm temperate, changing later in the early middle Eocene to subtropical to tropical…". He placed maximum mean annual paleotemperatures near 22°C and maximum mean annual paleoprecipitation near 140 cm in the middle Eocene, during the deposition of the Laney Member of the Green River Formation.

STRATIGRAPHIC FRAMEWORK

Abbreviations for institutions housing specimens are: National Museum of Natural History, Washington, D.C. (USNM); Florida Museum of Natural History, Gainesville, Florida (UF); University of California Museum of Paleontology, Berkeley, California (UCMP); Denver Museum of Natural History, Denver, Colorado (DMNH).

A generalized stratigraphic scheme is shown in Figure 5.2. Locality information is given in Figure 5.1 and Appendix 5.1 and a summary of collection data in Table 5.1. Strata bearing fossil floras were grouped into eight major sampling intervals for analysis (Fig. 5.2, Table 5.1). Samples (1-7) are from alluvial environments, while sample (8) is lacustrine: (1) the Tiffanian Bison Basin assemblage as reported by Gemmill and Johnson (1997); (2) the flora of the 18 m stratigraphic section through Big Multi Quarry (early Clarkforkian; Wilf et al., in press; (3) a time-averaged grouping of uppermost Fort Union Formation and lowest Wasatch Formation assemblages known or inferred to be Clarkforkian, including sample (2); (4) assemblages from the Main Body of the Wasatch Formation, from rocks of ?Graybullian to ?Lysitean age; (5) the flora of the Latham coal zone of the Ramsey Ranch Member of the Wasatch Formation in the eastern Great Divide Basin, from a single horizon of probable Lysitean age; (6) the flora of the Sourdough and Monument coal zones of the Ramsey Ranch Member of the central and eastern Great Divide Basin, of probable earliest Lostcabinian age; (7) the flora of the Niland Tongue of the Wasatch Formation in the north-central Great Divide Basin and the Vermilion Creek Basin, of middle-late Lostcabinian age; and (8) the flora of the uppermost Wilkins Peak Member of the Green River Formation, of earliest Bridgerian age.

Late Paleocene

Tiffanian data used here as sample (1) are as reported by Gemmill and Johnson (1997). Their study was of ten quarries exposed at a single stratigraphic horizon along about 0.6 km of strike in the Fort Union Formation of the Bison Basin, northern Great Divide Basin (Fig. 5.1). Fossil mammals found in the area have been assigned to Tiffanian zones Ti2, Ti3, and Ti5, indicating a range of possible ages from 59-60 to about 56.2 Ma (Gazin, 1956; Archibald et al., 1987; Prothero, 1995). Gemmill and Johnson inferred the environment of deposition as a shallow floodplain lake that filled rapidly with sediment.

For the Clarkforkian, the principal biochronologic tiepoint for southern Wyoming is Big Multi Quarry, in the northwestern Washakie Basin near Bitter Creek (Figs. 5.1, 5.3) (Rose, 1981a; Dawson and Beard, 1996; Wilf et al., in press). Big Multi Quarry is the most diverse Clarkforkian mammal locality known, and its 41 species indicate an early but not earliest Clarkforkian age (Wilf et al., in press). As an approximation, the quarry is shown in Fig. 5.2 at the Cf1/Cf2 boundary, placed in the latest calibrations of the Bighorn Basin sequence at ~55.7 Ma (Wing et al., 1999). Data from Big Multi Quarry and associated strata, sample (2), are as reported by Wilf et al. (in press).

Sample (3) contains 49 quarries of confirmed or probable Clarkforkian age exposed in the uppermost Fort Union Formation over a large area, including the Big Multi local section (Figs. 5.1, 5.3). Some of these quarries are known to be Clarkforkian based on mammalian occurrences. My tentative assignment of the remainder to the Clarkforkian is primarily based on high stratigraphic position in the Fort Union Formation, floristic similarity to known Clarkforkian strata, and the use of a megafloral zonation established in the Bighorn Basin (Hickey, 1980; Wing, 1998). In the Bighorn Basin, the Clarkforkian and earliest Wasatchian are congruent with the *Persites-Cornus* “Zone” (PCZ). The PCZ is characterized by the mutual first appearances of *Persites argutus* and *Cornus hyperborea* as well as the first appearances of *“Cinnamomum” sezannense*, *Ternstroemites aureavallis*, and *Zingiberopsis isonervosa,* and the reappearance of palm leaves and cycads. A feature of the upper PCZ, which begins within the middle Clarkforkian (Cf2), is the dominance of *Corylites* sp. leaves (= Betulaceae sp. 1 *sensu* Wing, 1998) in association with *Palaeocarpinus aspinosa* fruits. Wilf et al. (in press) found that the composition of the plant assemblage of the Clarkforkian Big Multi section was consistent with the PCZ, suggesting that the PCZ may be correlatable across Wyoming. An important exception is that *Corylites* in association with *P. aspinosa* was already dominant in southern Wyoming in the Tiffanian Bison Basin flora and the early

Clarkforkian Big Multi local section (Gemmill and Johnson, 1997; Wilf et al., in press). *Corylites* dominance was therefore not used to diagnose the PCZ in the study area.

The following areas of the uppermost Fort Union Formation around the Rock Springs Uplift have yielded plant localities of known Clarkforkian age (Figs. 5.1, 5.3; Appendix 5.1): (1) the Big Multi local section; (2) exposures along the Union Pacific railroad tracks southwest of Bitter Creek; and (3) a portion of the Sand Butte Rim NW section of Roehler (1977), about 10 km southwest of Big Multi Quarry. Fossil plants from these strata are also entirely consistent with the PCZ. The following are of probable Clarkforkian age: (1) exposures on the south flank of the Rock Springs Uplift, primarily on the south slopes of the Brooks Draw drainage east of Potter Mountain, in the Potter Mountain 7.5’ Quadrangle; and (2) exposures on the west flank of the Rock Springs Uplift.

Both the Sand Butte Rim NW and Union Pacific study areas lie directly on strike with Big Multi Quarry, although exact correlation at the level of beds is not possible (Fig. 5.3). Clarkforkian age of the upper two of the three plant beds in the Sand Butte Rim NW section is confirmed by the presence of both champsosaur and rodent fossils (Roehler, 1979). The lowermost bed contains *Ternstroemites aureavallis*, which has a Clarkforkian first appearance in the Bighorn Basin.

The Brooks Draw quarries are primarily in a carbonaceous shale/siltstone layer that is laterally extensive over more than 2 km (13 quarries). This layer lies at varying stratigraphic distance beneath a pronounced scour contact with the overlying Wasatch Formation Although there are no faunal data, this horizon is highly similar sedimentologically and floristically to that described by Wilf et al. (in press) at the 18 m level of the Big Multi section. All but three species from this unit are found in the Big

Multi section; these three are also singletons. Both *Persites argutus* and *Cornus hyperborea* are present and locally abundant. The strong similarity of the flora to that of the Big Multi section, in combination with the fact that the 18 m level of the Big Multi section and the carbonaceous shale layer in the Brooks Draw section are the only laterally extensive (> 1 km) carbonaceous shale units found in the uppermost Fort Union Formation of the Rock Springs Uplift suggests that the two units are approximate age equivalents (Fig. 5.3).

A channel deposit approximately 110 m below the Brooks Draw carbonaceous shale layer contains both *Persites* and *Cornus* as well as palm leaves and is taken as Clarkforkian but older than Big Multi Quarry (USNM loc. 41292; Fig. 5.3). This is corroborated by the only appearance in this study of "*Viburnum*" *cupanioides,* which has a Cf1 last appearance in the Bighorn Basin, and by the local abundance of "*Viburnum*" *antiquum*, which, within the Clarkforkian, is only abundant in the earliest Clarkforkian of the Bighorn Basin (Wing, 1998). Additional material from this area was collected west of the Brooks Draw section (Fig. 5.1).

On the west flank of the Rock Springs Uplift, five quarries in badlands near the mouth of the Little Bitter Creek drainage yielded small collections. However, *Cornus* and *Persites* were both found. A sixth quarry from this drainage is the megafossil locality reported by Kirschbaum (Kirschbaum, 1987; USNM loc. 41277; Fig. 5.1), which is located in the lowest Wasatch Formation but is known to be Paleocene from pollen data (Kirschbaum and Nelson, 1988).

A locality within Rock Springs (USNM loc. 41278, UF loc. 18126, DMNH loc. 15270; Figs. 5.1, 5.3) occurs in an indurated, calcareous sandstone, close to the Fort Union-Wasatch contact. This is the most diverse site in the Fort Union Formation in the study area (16 species), and it contains 10 dicot species not found in the other 48 quarries. Age assignment is difficult because the locality is an isolated exposure in the largely covered valley of Killpecker Creek, and plants are the only fossils yet recovered. *Cornus* is abundant and “*Cinnamomum” sezannense* is present, which indicate a Clarkforkian age. *“Viburnum*” *antiquum* is abundant, indicating an early Clarkforkian age at youngest, perhaps similar to USNM loc. 41292 (Fig. 5.3).

Taken together, these 49 quarries within the uppermost Fort Union Formation probably represent vegetation from early to ?middle Clarkforkian time. Given the possibility of northward floral migration at this time (Wilf et al., in press), some of the older quarries with composition that matches the PCZ, especially USNM locs. 41292 and 41278, may be latest Tiffanian. It is unlikely that late Clarkforkian floras are included because none of the quarries in the sample appear to be much higher stratigraphically than rocks in the Big Multi local section (Fig. 5.3). The recent discovery of a middle Clarkforkian (Cf2) fauna in the Great Divide Basin offers the possibility that even younger Paleocene megafloras may be found in the area (Anemone et al., 1996).

Early Eocene

Plant fossils from the Main Body of the Wasatch Formation are extremely rare. A portion of the lower Wasatch Fm. in the Dry Canyon area on the west side of the Rock Springs Uplift is Paleocene on the basis of pollen data (Kirschbaum, 1987; Kirschbaum and Nelson, 1988). However, the base of the Wasatch Fm. contains diagnostic Wasatchian mammals in the Washakie Basin reference section on the southeast side of the uplift, closer to the plant localities in question (Roehler, 1992b; Figs. 5.2, 5.3). Lithologies are sandy and frequently oxidized, and the occasional fine-grained carbonaceous deposits are localized and highly weathered. The six quarries found and combined here as sample (4) were depauperate (Figs. 5.1, 5.3; Appendix 5.1). Five are in the basal Wasatch Formation in the Brooks Draw section (Fig. 5.3). One is located at approximately the 288 m level of the Wasatch Formation by correlation to the Washakie Basin reference section (Roehler, 1992b; Fig. 5.3).

A significant datum in the Main Body that may be isochronous across Wyoming is the FAD of *Hadrianus*, a large tortoise (Hutchison, 1980; Fig. 5.2). This datum in the Bighorn Basin occurs at the base of the *Bunophorus* Interval-Zone, or terminal Graybullian (Schankler, 1980; P. Holroyd, pers. comm., 1998), approximately 53.4 Ma in the calibration of Wing et al. (1999).

Productive horizons were found within the Ramsey Ranch Member and Niland Tongue of the Wasatch Formation in the extensive coal fields of the Great Divide Basin (Pipiringos, 1961; Masursky, 1962; Roehler, 1987, 1991, 1992a, 1993). I also discovered quarries of very limited diversity in the Ramsey Ranch Member of the Washakie, Vermilion Creek, and Green River Basins and the Niland Tongue of the Vermilion Creek Basin. All of these together only added one new morphotype to the analysis ("Monocot A"); the sites are listed in Appendix 5.1 but will not be analyzed further.

The lowest productive level within the Ramsey Ranch Member was sample (5), a tabular carbonaceous shale layer immediately above the Latham 4 coal *sensu* Masursky (1962; Figs. 5.1, 5.2). The Latham coal zone is the oldest in the Great Divide Basin sequence (Masursky 1962). Preservation was moderately poor in this interval, and most of the outcrops were highly weathered. However, the fossiliferous units were fine-grained, indicating little transport of plant material.

Outstanding plant fossils were recovered from the uppermost Ramsey Ranch Member in roof strata of coal zones below the Luman Tongue of the Green River Formation. These units have been named differently by Pipiringos (1961) and Masursky (1962), working in the central and eastern Great Divide Basins, respectively. Both authors refer to the first coal zone below the Green River Formation as the Monument coal zone. However, the next coals below the Monument zone are referred to the Larsen and Sourdough coal zones by Masursky, and these same are equal to the Tierney coals of Pipiringos. Furthermore, the Sourdough coal coalesces with the overlying Monument coal over much of the area mapped by Masursky. I have chosen to lump all of these units for analysis because (1) levels that bear fossil plants are minimally separated stratigraphically (0-10 m); and (2) nearly all of the plant species recovered can be found within a single extensive layer above the Sourdough 2 coal. To simplify nomenclatural issues, I will refer to this package as the “Sourdough assemblage”, sample (6). This choice is made with respect both to the fossiliferous Sourdough coal zone and to Sourdough Butte (“Coal Butte” on some topographic sheets), which bears some of the most productive fossil plant beds in fine sandstones immediately above the Sourdough 2 coal. The latter is thick and laterally extensive over much of the Great Divide Basin study area and will be used here as a stratigraphic reference point for the Sourdough assemblage. Additional collections from the east end of Sourdough Butte have been made by crews from the Denver Museum of Natural History (DMNH loc. 94).

Faunal locality no. 15 of Pipiringos (1961: Table 5.2), just northeast of Tipton Buttes and 80 m below the base of the Green River Formation, is under study by Anemone and others (Anemone et al., 1996). Preliminary faunal lists contain elements that are considered diagnostic of both the Lysitean and Lostcabinian subages (R. Anemone, pers. comm., 1998). I provisionally correlate the Sourdough 2 coal, which lies 42 m above the fauna, to the 621 m level of the Elk Creek section, where a laterally extensive carbonaceous shale deposit occurs that is also rich in fossil plants (e.g., Davies-Vollum and Wing, 1998). The 621 m level is earliest Lostcabinian and has been calibrated to 52.8 Ma (Wing et al., 1999). This interbasinal correlation is based primarily on high floristic similarity, including a large number of first appearances of the same plant species in both the southern and northern sections, which will be discussed later. It is also based on the Lysitean/Lostcabinian age of the underlying Tipton Buttes fauna. The correlation is intended to suggest approximate, not exact age equivalence. The Latham plant assemblage lies approximately 48 m below the Tipton Buttes fauna and is most likely Lysitean.

Identifiable macroflora from the Niland Tongue of the Great Divide Basin, sample (7), is rare. Nearly all material used was found at two previously known localities in the upper 27 m of the Niland Tongue on the north rim of Lost Creek Flat, USNM locs. 41361 and 41362 (see Pipiringos, 1961: Table 2; Wing and Hickey, 1984). These are stratigraphically separated by 18 m (Pipiringos, 1961: Table 2) and are lumped for this analysis. The age of the Niland Tongue is Lostcabinian on the basis of fossil mammals (Gazin, 1965; Roehler, 1987; Krishtalka et al., 1987). Precise age assignment is not possible given present data. However, lithostratigraphic interpolation can be used within the Lostcabinian, which is radiometrically calibrated. The base of the Lostcabinian is currently placed at 52.9 Ma (Wing et al., 1999), and the end is estimated to be 50.1-50.2 Ma based on recalibrated K/Ar dates (Krishtalka et al., 1987; Clyde et al., 1997). Stratigraphic interpolation based on the Washakie Basin and Green River Basin reference sections (Roehler, 1992b) and using the Tipton Buttes fauna as the base of the Lostcabinian gives an approximate duration of the Niland Tongue of 0.5 my, from ~52.3-51.7 Ma. 51.7 Ma is used here provisionally for the Niland Tongue assemblage (Fig. 5.2).

The fossil flora from the uppermost Wilkins Peak Member and lowermost Laney Member of the Green River Formation on the southwest slope of Little Mountain (Fig. 5.1) was first collected in 1963 by MacGinitie (1969; UCMP loc. PA 116). While it has not been possible to relocate MacGinitie's original quarry, two additional quarries have been collected in the same area at what is thought to be the same stratigraphic level (UF loc. 15882 = USNM loc. 41427; USNM loc. 41370; Fig. 5.1; Appendix 5.1). All of the Little Mountain collections were examined for this analysis. A site in the upper Wilkins Peak Member on White Mountain yielded a single specimen of a species not found at Little Mountain, *Equisetum* sp. (USNM loc. 41368; Fig. 5.1; Appendix 5.1).

K-Ar dates from the Big Island Tuff, in the Wilkins Peak Member inside the Stauffer trona mine in the Green River Basin, and tuff RLM 4-70, from the upper third of the Wilkins Peak Member near Green River (Mauger, 1977), have been recalibrated to 50.1 and 50.2 Ma, respectively, the dates used to estimate the age of the Wasatchian/Bridgerian boundary (Krishtalka et al., 1987; Fig. 5.2). The Little Mountain assemblage, which is from the uppermost Wilkins Peak Member, therefore dates from approximately 50 Ma and is both early Bridgerian and late early Eocene in age (Cande and Kent, 1992).

METHODS

Collection and processing procedures for plant fossils were identical to those detailed in Wilf et al. (in press) and will only be outlined here. All fossils were recovered by surface prospecting and quarrying. The 120 individual quarries were each highly local, consisting of 1-2 m^3 of sediment (Fig. 5.1; Appendix 5.1). With the following exceptions, all plant fossil material was collected by myself and is housed in the Department of Paleobiology, USNM, Accession no. 420051. The 10 Bison Basin quarries were collected by DMNH field crews, as discussed by Gemmill and Johnson (1997). Additional material was examined from other institutions: (1) UF and DMNH collections from the Rock Springs site; (2) the Little Mountain collections discussed by MacGinitie (1969; UCMP loc. PA 116) and subsequent UF collections from the same stratigraphic level (UF loc. 15882). I note that the floral composition of MacGinitie's collections from the lowermost Laney Member was essentially identical to that of the uppermost Wilkins Peak Member, only adding a single pinaceous seed type.

The majority of the quarries were in fine-grained rocks, predominantly carbonaceous shales and siltstones of distal backswamps and oxbows but also fine-grained to occasionally medium-grained near-channel or lake margin sandstones (Appendix 5.1; Table 5.2). Plants were preserved exclusively as compression-impression assemblages, primarily of leaves, but also including fruits, seeds, flowers, cones, axes, and rhizomes. Leaf assemblages from carbonaceous shales in the late Paleocene and early Eocene of the Bighorn Basin are considered to be minimally transported and to represent 2000 years or less of deposition (Davies-Vollum and Wing, 1998). The carbonaceous shale and siltstone beds throughout the study area are highly similar in general features to those in the Bighorn Basin and are also considered to represent "snapshot" assemblages from a local source (Wilf et al., in press; Davies-Vollum and Wilf, unpublished data). While a detailed taphonomic and sedimentological analysis is beyond the scope of this paper, other major features indicating minimal transport at the majority of quarry sites are (1) high organic carbon content (Wilf et al., in press), fine grain size, and lack of primary current features; (2) frequent preservation of fine leaf features, including cuticle, the highest orders of venation, and detailed insect mines; and (3) frequent occurrence of several leaf sizes, including large leaves, on a single bedding plane, indicating little hydraulic mixing. Even the sandier environments preserve many whole leaves and have few overturned or ripped leaves, indicating little transport (Wilf et al., in press). The lacustrine Little Mountain assemblage differs taphonomically from the others, which are fluvial. Lacustrine assemblages of fossil plants are widely thought to represent somewhat longer time windows than fluvial assemblages and to be derived from a significantly larger source area (e.g., Wing and DiMichele, 1995).

Fossil plants were examined and compared to collections of comparative fossil material from this time period held at USNM, the National Cleared Leaf Collection (housed in the Department of Paleobiology, USNM), and the U.S. National Herbarium. The result was 203 morphotypes, including the morphotypes from the Bison Basin study: 165 leaf types, 37 reproductive types, and *Equisetum* sp. axes (Tables 5.1, 5.3). Fossil leaf morphotypes were designated primarily on the basis of rigorous analysis of leaf architecture (Hickey, 1973, 1979; Hickey and Wolfe, 1975). Morphotypes were either assigned to previously described forms, placed within taxonomic groups with varying degrees of confidence, or classified as *incertae sedis* (Table 5.3). I have designated a reference specimen with a museum catalogue number for each morphotype (Table 5.3). Several leaf morphotypes were found to be identical to undescribed forms collected and referenced by S. L. Wing and housed in USNM collections (Wing et al., 1995; Wing, 1998); I have indicated Wing's informal names for these taxa whenever possible (Table 5.3). My best estimate of the number of biological species represented is 167 (Table 5.1). The flora contains a large number of undescribed taxa as well as abundant new and informative material of previously known species, and formal descriptive work will be the subject of future papers. In the meantime, preliminary descriptions and digital images of all of the morphotypes are available to interested researchers in electronic format from myself. A complete presence-absence matrix for all morphotypes and quarries is available from the GSA Data Repository.

Field censuses of dicot leaves were taken for quarries with abundant identifiable material as in Wilf et al. (in press). As discussed in a number of publications, leaf count data from 350-400 minimally transported fossil dicot leaves are thought to reflect relative biomass dominance within the source forest (Burnham et al., 1992; Gemmill and Johnson, 1997; Davies-Vollum and Wing, 1998; Wilf et al., in press). Census data for the ten Bison Basin quarries are as reported by Gemmill and Johnson (1997), except that I have modified these data to include only dicots as in Wilf et al. (in press). Within the lumped Clarkforkian sample are ten censused quarries, including the four censuses from the Big Multi section reported by Wilf et al. (in press; Table 5.4). Smaller leaf counts were used at depauperate sites (Table 5.4). Five quarries were censused from the Sourdough assemblage (Table 5.5). Sufficient plant material for censuses was not available in the Main Body, the Latham coal zone, or the Niland Tongue of the Wasatch Formation. The Little Mountain assemblage is not directly comparable to the others because of the lacustrine depositional setting, and no field census was attempted there. The census process did not tend to add significantly to species counts for a site, as I had usually recovered most of the species at each quarry in preliminary excavations. Also, many census quarries were as species-poor as uncensused sites (Tables 5.5, 5.6). For these reasons, I consider censused and uncensused quarries alike to have been approximately equally sampled for species composition.

Diversity indices based on leaf counts, to the extent that leaf counts reflect relative biomass, represent the evenness of the relative abundance of species within the source forest (Wilf et al., in press). Simpson and Shannon diversity indices were calculated for each censused quarry (Tables 5.1, 5.5, 5.6). For the Latham assemblage, only cumulative diversity indices based on a lumped drawer count of all localities are included in Table 5.1 because of the small total sample size (226 leaves). There is no collecting bias in this count because all identifiable material was collected from these quarries.

Paleoclimate analysis was based on a synthesis of all available evidence. I used two primary approaches, supplemented by available sedimentological indicators: (1) analysis of the climatic tolerances of the nearest living relatives (NLRs) of extinct organisms; and (2) quantitative analysis of leaf morphology. The merits and shortcomings of each approach have been examined elsewhere (e.g., Chaloner and Creeber, 1990; Wing and Greenwood, 1993; Wolfe, 1995; Herman and Spicer, 1997; Mosbrugger and Utescher, 1997). The NLR approach is considered (1) most applicable when the fossil organism belongs to a diverse, widespread, extant clade with consistent climatic tolerances; (2) to increase in accuracy as more organisms are analyzed; and (3) to decrease in accuracy with increasing age of the fossils. Paleogene plants were phylogenetically close to extant taxa in comparison to the Mesozoic, and the NLR and leaf-morphologic approaches have shown broad agreement with each other and with other proxies in many studies of this time period (Hutchison, 1982; Johnson and Hickey, 1990; Wolfe, 1992; Wing and Greenwood, 1993; Greenwood and Wing, 1995; Wing et al., 1999; Wilf et al., in press).

Two quantitative approaches were used to infer paleoclimates, leaf-margin analysis (Wolfe, 1979; Wing and Greenwood, 1993; Wilf, 1997) and leaf-area analysis (Wilf et al., 1998). Both approaches use only the woody dicotyledons in an assemblage. For each sampling level, the number of woody dicots and paleoclimatic data are shown in Table 5.1. Leaf-margin analysis uses the following linear relationship between mean annual temperature (MAT, in °C) and the proportion P of species in a sample with untoothed margins, based on the East Asian data set of Wolfe (1979) and quantified by Wing and Greenwood (1993): estimated MAT = $30.6P + 1.14$. The binomial sampling error on this estimate nearly always exceeds the published regression error of 0.8°C and is used here as a minimum error of the estimate (Wilf, 1997: eq. 4; Table 5.1).

Leaf-area analysis is based on the highly significant relationship between the mean natural logarithm of the species' leaf areas in a sample (MlnA, where area is measured in square millimeters) and mean annual precipitation (MAP, in centimeters): ln (estimated MAP) = 0.548 MlnA + 0.768, standard error = 0.359 (Wilf et al., 1998). The quantity MlnA was based on the percentage of species found in each of the Raunkiaer-Webb discrete leaf area categories (Webb, 1959), using the formulae of Wilf et al. (1998). If a species displayed more than one leaf area category, it received a fractional score for each category, including rangethroughs. For example, a species found in both the microphyll and mesophyll categories received a score of 1/3 for each of microphyll, notophyll (the intervening category), and mesophyll. Because of the high sensitivity of recovered leaf size to taphonomic processes and hydraulic sorting, paleoprecipitation estimates from leaf-area analysis must be considered approximate at best. However, it is my judgment that intensive sampling throughout the section, the abundance of minimally transported material, and the abundance of large leaves at many localities ensures that a nearly complete size spectrum has been recovered at least for the most common species.

FLORAL TURNOVER

Two major floral turnovers affecting over 80% of species are recorded (Table 5.3). The first occurred from the Clarkforkian to the middle Wasatchian. The second took place during the Wasatchian-Bridgerian drying interval. While these species-level extinctions were severe, higher-level taxa show little turnover and demonstrate two prominent immigration events of families with modern tropical affinities, one each in the Clarkforkian and middle Wasatchian (Table 5.3).

Species turnover

Tiffanian vegetation in Bison Basin featured several forms known from Paleocene rocks elsewhere in the Rocky Mountains and Great Plains (Gemmill and Johnson, 1997): "*Ampelopsis*" (*Archeampelos*) *acerifolia*, *Corylites* sp. and *Palaeocarpinus aspinosa*, *Equisetum* sp., *Fortuna* cf. *Fortuna marsilioides, Joffrea speirsii*, *Metasequoia occidentalis*, *Platanus raynoldsi*, "*Viburnum" asperum*, "*Viburnum" cupanioides*, and possibly "*Carya*" *antiquorum.* All of these taxa persist into the Clarkforkian of the study area, excepting *cf. F. marsilioides* and *P. raynoldsi*. However, disappearance of the latter is probably a sampling artifact, as a possibly conspecific form appears in the Bridgerian Little Mountain assemblage, and the species is also known from early Paleocene to Lostcabinian strata in the Bighorn Basin (Table 5.3). Examination of specimens of the undescribed taxa found at Bison Basin in DMNH collections did not reveal other forms that ranged into the Clarkforkian.

Many species with Clarkforkian first appearances in the Bighorn Basin (Hickey, 1980; Wing, 1998) also first appear in the study area in rocks of demonstrated

Clarkforkian age: *Averrhoites affinis*, *Cornus hyperborea*, *“Cinnamomum” sezannense*, aff. *Ocotea* (probably equal to the Bighorn Basin morphotype *Phoebe* sp. of Wing 1998), *Persites argutus*, *Zingiberopsis isonervosa*, palm leaves, and cycads, as well as *Ternstroemites aureavallis* in the lowermost plant bed of the Sand Butte Rim NW section, 18 m below Clarkforkian mammals (Fig. 5.3). All of these taxa therefore appear to be useful indicators of Clarkforkian or younger age throughout Wyoming. In addition, palm leaves, cycads, and the fern *Allantodiopsis erosa* reappear in the Bighorn Basin in the Clarkforkian following a Tiffanian hiatus; these also are absent from the Tiffanian of the study area but present in the Clarkforkian. However, the arrival of new forms did not greatly affect the dominant species (Gemmill and Johnson, 1997; Wilf et al., in press). Species turnover from the Tiffanian to the Clarkforkian was high (87% first appearances; 79% last appearances). As the minor species are the least likely to be sampled, these high percentages may be sampling artifacts.

Floral data from the Main Body of the Wasatch Formation are very poor. The lowest units of the Wasatch Formation above the Fort Union-Wasatch unconformity in the Brooks Draw section contain taxa typical of the Paleocene (Fig. 5.3): *“Carya” antiquorum*, *Corylites* sp., and *Metasequoia occidentalis*. The only other locality in the Main Body, USNM loc. 41311 (Figs. 5.1, 5.3) has *Averrhoites affinis* and *Zingiberopsis isonervosa*, forms that are found both in the Paleocene and Eocene of the area. As poor as the record is from the Main Body, it supports a scenario in which some Paleocene species persisted into the earliest Eocene. No diagnostically Eocene plant macrofossils, such as *Platycarya*, were found at the handful of Main Body localities.

By Latham time a major turnover clearly had occurred in plant communities (Table 5.3). Only a handful of species remain from the Clarkforkian: *Averrhoites affinis*, *Zingiberopsis isonervosa*, and palm leaves of no certain affinity to those found in the Clarkforkian. The most abundant form, however, is “*Meliosma*” *longifolia*, which ranges from the Tiffanian to the late Graybullian in the Bighorn Basin and is also found both in the Clarkforkian and Graybullian of the Golden Valley Formation of North Dakota (Hickey, 1977; Wing, 1998). The rest of the assemblage consists of immigrants, including these characteristically Eocene taxa: *Alnus* sp., Apocynaceae sp., *Cnemidaria magna*, *Dombeya novi-mundi*, *Lygodium kaulfussi*, *Platycarya* sp. (undiagnostic leaflets, most likely to be *P. americana* because this species occurs higher in the section), *Salvinia preauriculata*, and possibly *Stillingia casca*.

In the early Lostcabinian Sourdough assemblage the few holdovers from the Paleocene are *Averrhoites* and *Zingiberopsis*, plus the “returns”, probably due to better preservation, of *Equisetum, Glyptostrobus europaeus*, *Macginitiea gracilis*, and sterile foliage of *Woodwardia.* Also, *Chaetoptelea microphylla* occurs at one quarry (USNM loc. 41341), a taxon not found in the Paleocene of this study but reported from Tiffanian to Lysitean strata of the Bighorn Basin and from the Golden Valley Formation. The percentages of species making first and last appearances from the Clarkforkian to Sourdough time are 89% and 87%, respectively.

The Sourdough assemblage shares many species with the megaflora recovered from the tabular early Lostcabinian carbonaceous shale at the 621 m level of the Elk Creek section in the Bighorn Basin (Davies-Vollum and Wing, 1998; Wing, 1998). This floristic similarity is strong evidence for the previously discussed correlation of the two horizons and an early Lostcabinian age for the Sourdough assemblage (Fig. 5.2). Taxa that first appear both in the Sourdough assemblage and at the 621 m level of the Elk Creek section are: *“Eugenia” americana*, aff. Sapindaceae sp. 2 (=”Dicot XXXI” of Wing, 1998), aff. *Schoepfia republicensis*, “Tatman fern”, dicot RR48 (= “Dicot XXXVI” of Wing et al., 1995) and dicot RR27 (= “Dicot XXXVII” of Wing, 1998). Additional shared species are: *Alnus* sp., Apocynaceae sp. (FAD at 621 m in Elk Creek section), *Cnemidaria magna*, “*Dombeya*” *novi-mundi*, *Populus wyomingiana*, aff. *Sloanea,* and *Thelypteris iddingsi.* Dominant or abundant species in both samples are *Alnus* sp., *Cnemidaria magna*, “*Dombeya*” *novi-mundi*, *Lygodium kaulfussi*, and “Tatman fern”. I note that *Platycarya* leaflets are present in both assemblages, but that *P. castaneopsis* occupied the Bighorn Basin and *P. americana* the study area. In a survey of *Platycarya* spp. In North America, Wing and Hickey (1984) noted that *P. americana* appeared to be restricted to areas east of the Front Range; its geographic range is extended here.

The Sourdough assemblage contains several species known from the middle Eocene Wind River flora of west central Wyoming and primarily middle Eocene Green River flora of southern Wyoming, northern Colorado, and northern Utah (MacGinitie, 1969; MacGinitie, 1974). These are *“Eugenia” americana*, *Populus wyomingiana*, and *Thelypteris iddingsi*, and possibly *Dendropanax latens* . Also, a menispermaceous fruit is present that may be conspecific with *Atriaecarpum clarnense*, known from the middle Eocene Clarno Formation of Oregon (Manchester, 1994).

The Niland Tongue sample demonstrates no substantial turnover since Sourdough time. This is not surprising given that the environments of deposition of the Ramsey Ranch Member and the Niland Tongue are nearly identical (Roehler, 1993). Elements present at both levels are *Alnus* sp., *Averrhoites affinis* (persistent since the Paleocene), aff. *Dendropanax latens*, “*Dombeya*” *novi-mundi*, *Lygodium kaulfussi*, *Populus wyomingiana*, *Salvinia preauriculata*, *Thelypteris iddingsi, Zingiberopsis isonervosa,* palm leaves, and possibly aff. *Schoepfia republicensis*. Two species make first appearances that are known from the middle Eocene Wind River flora: *Acrostichum hesperium* and *Proteaciphyllum minutum*. Both leaflets and fruits of *Platycarya castaneopsis* are abundant in the Niland Tongue of the Great Divide Basin, documenting the Great Divide Basin as the only area where both known fossil species of *Platycarya* are unequivocally present as macrofossils.

The Wilkins Peak assemblage documents a second major species turnover in the area. Only a handful of taxa are found that were present lower in the section: *Averrhoites affinis, Equisetum, Glyptostrobus europaeus*, and possibly *Platanus raynoldsi*, still persisting from the Paleocene, and from the Wasatchian, *Alnus sp.*, "*Eugenia*" *americana, and Proteaciphyllum minutum*. In addition, *Lygodium kaulfussi* must have remained in the area because it occurs in the overlying Bridger Formation and Laney Member of the Green River Formation (Manchester and Zavada, 1987; author's collections). Counting *L. kaulfussi* as a holdover, 83% of the Wilkins Peak species are first appearances. The floristic affinities of the assemblage are strongly with Rocky Mountain floras from the middle and late Eocene, especially the Green River, Wind River, and Florissant floras (MacGinitie, 1953, 1969, 1974). The most abundant elements, based on drawer counts, are *Parvileguminophyllum coloradensis*, *Rhus nigricans*, and *Cedrelospermum nervosum*.

Turnover of families

Although systematic knowledge of the flora is preliminary (Table 5.3), it is nevertheless possible to discern floristic patterns at high taxonomic levels in the sequence. The Betulaceae, Equisetaceae, Juglandaceae, Platanaceae, and Taxodiaceae are present throughout the section. The Betulaceae, Cercidiphyllaceae, Cornaceae, Juglandaceae, and Taxodiaceae were conspicuous elements in the

Tiffanian and Clarkforkian floras. These families are well known throughout the Paleocene (e.g., Brown, 1962) and mostly have temperate distributions and are deciduous today, therefore traditionally associating the Paleocene with “temperate” conditions. In the Clarkforkian, the “temperate” families retained their importance as a number of new groups arrived or reappeared after a hiatus: Arecaceae, Cycadaceae, Lauraceae, Magnoliaceae, Malvaceae-Sterculiaceae-Bombacaceae, Myrtaceae, Theaceae, and Zingiberaceae. All of these families have maximum diversity in the tropics today, and all but the Lauraceae and Magnoliaceae are rare to absent in living temperate forests.

The Wasatchian flora of the Great Divide Basin documents the persistence of many families from the Paleocene (Table 5.3). The Betulaceae remained dominant, but *Alnus* replaced *Corylites*. Juglandaceae also persisted, but in the form of *Platycarya* spp., not the Paleocene “*Carya*” *antiquorum*. The Malvaceae-Sterculiaceae-Bombacaceae complex and Myrtaceae were represented by “*Dombeya*” *novi-mundi,* a dominant element, and “*Eugenia*” *americana*, respectively. Other families continuing to inhabit the area were the Arecaceae, Blechnaceae, Cycadaceae, Lauraceae, Magnoliaceae, Polypodiaceae, and Ulmaceae. In addition to these groups with phylogenetic links to the Paleocene, a number of families new to the region arrived in the Wasatchian, including members of the Apocynaceae, Cyatheaceae, Leguminosae, Menispermaceae, and Salviniaceae, as well as morphotypes with strong architectural similarity to the Araliaceae, Elaeocarpaceae, Euphorbiaceae, Olacaceae, and Sapindaceae. Nearly all of the preceding groups have tropical centers of distribution today.

Despite high species turnover from the Wasatchian, the Wilkins Peak sample also records the persistence and/or increased richness of many families from the

Wasatchian and before (Table 5.3). These include the ?Araliaceae, Betulaceae, Euphorbiaceae, Juglandaceae, Lauraceae, Leguminosae, Myrtaceae, Platanaceae, Salicaceae, and Ulmaceae. The only families making a clear first appearance as megafossils at this level are the Anacardiaceae, Fagaceae, Pinaceae, and Simaroubaceae, although the latter was present as palynomorphs in the Wasatchian Niland Tongue (Nichols, 1987).

PALEOCLIMATE AND PALEOENVIRONMENT

Evidence from nearest living relatives and quantitative analyses of fossil leaves, combined with available faunal and sedimentological evidence, demonstrates several profound changes in regional climate from the Tiffanian to the Bridgerian (Fig. 5.4; Table 5.1).

The Bison Basin assemblage has no taxa associated with warm conditions but several that indicate wet environments. The latter includes the horsetail *Equisetum* and the aquatic fern *Fortuna* cf. *F. marsilioides*. Ferns and horsetails rely on free-living haploid generations that are highly vulnerable to desiccation and also require aqueous fertilization. Horsetails in particular are physiologically restricted to wet habitats because their thin-walled, small, photosynthetic spores remain viable for no more than two weeks when dry (Lebkuecher, 1997). Palms and gingers, which have very limited frost tolerance, are conspicuously absent. Floristic affinities of the Bison Basin dicots are primarily with modern temperate forests. Leaf-margin analysis indicates mean annual temperatures of 12.6°C (Fig. 5.4; Table 5.1).

In the Clarkforkian there is clear evidence of humid and subtropical conditions (Wilf et al., in press). Palms, the ginger *Zingiberopsis*, and cycads are present, as well as a large number of immigrant dicot families with modern tropical affinities (Table 5.3).

Palms are taken as evidence of climates with mean annual temperature > 10°C, cold month mean temperature > 5°C, and yearly minimum temperature > -10°C (Greenwood and Wing, 1995). The Zingiberaceae are a diverse and entirely tropical group today (Heywood, 1993). Living cycads are a relict group of entirely tropical distribution, although an extinct genus, *Nilssoniocladus*, was deciduous and inhabited polar regions in the Cretaceous (Spicer and Herman, 1996). Two genera of crocodilians have been found at Big Multi Quarry (Rose, 1981a), as have champsosaurs both at Big Multi Quarry and the Clarkforkian vertebrate quarry in the Sand Butte Rim NW section (Roehler, 1977, 1979; Rose, 1981a; Fig. 5.3). Crocodilians are taken as evidence for coldest-month mean temperatures of >7°C, mean annual temperatures of >16°C, and mean annual temperature ranges of <21.1°C (Markwick, 1994). Leaf-margin analysis indicates mean annual temperatures of 14.7°C for the lumped Clarkforkian sample and 19.5°C for the Big Multi section (Fig. 5.4; Table 5.1). Although the error bars overlap, the higher estimated MAT and the younger age of the Big Multi section relative to some of the Clarkforkian localities provide evidence for warming within the Clarkforkian.

Evidence for moist Clarkforkian conditions compiled by Wilf et al. (in press) from the Big Multi section included: (1) presence of a variety of hydrophilic biota: two species of ferns, a horsetail (*Equisetum*), salamanders, champsosaurs, crocodilians, and a pantolestid; (2) closed, forested conditions sustainable only with ample rainfall, implied both by a high diversity of arboreal mammals, including 11 primatomorphs, and by cenogram analysis; (3) sedimentologic criteria uniformly indicating wet conditions with little seasonality of precipitation, including the presence of gray, hydromorphic, “simple” paleosols, dark coals, and natrojarosite, and the lack of red beds and paleosol carbonates (Kraus and Aslan, 1993; Davies-Vollum, 1996; Davies-Vollum and Wing, 1998). These lithologies are also present throughout the upper Fort Union Formation in the study area. Leaf-area analysis gives essentially identical MAP estimates for the Big Multi section (137 cm) and for the lumped Clarkforkian sample (142 cm).

A change in depositional environment from the upper Fort Union Formation to the Main Body of the Wasatch Formation is strongly indicated by the nearly complete absence of coals in the Main Body and the presence of true red beds on the edges of the Greater Green River Basin, contrasted with chloritic green and gray beds in basin centers (Roehler, 1992b). I have also recovered abundant paleosol carbonates from red beds in the Main Body of the northwestern Great Divide Basin that are Graybullian in age, based on nearby fossil mammals (Pipiringos, 1961: 13), further indicating increased drainage and seasonal moisture deficits (Arkley, 1963; Sobecki and Wilding, 1982). All of these lithologic changes appear to reflect increasing floodplain relief and some regional drying as surrounding uplifts became more active and created rain shadows, so that only the central basins remained waterlogged through most of the year (see Roehler, 1993).

The scattered proxy record from the Main Body of the Wasatch Formation suggests continuation of mild conditions with pronounced warming in the upper third of the Main Body. There is no significant gap in the crocodilian record in the Main Body (P. Holroyd, pers. comm. 1998), indicating that severe winters were rare at any time. Pollen work by Leopold and Roehler (in Roehler, 1992b) shows palm pollen to be present at the 225 m level of the Washakie Basin reference section in the same sample as the FAD of *Platycarya* pollen (Fig. 5.3) and to continue to be present to the top of the Main Body. *Zingiberopsis* foliage occurs at USNM loc. 41311 at ~288 m (Fig. 5.3). An increase in *Platycarya* pollen abundance occurs within the Main Body from its FAD to 36% of palynomorphs at 374 m (Figs. 5.2, 5.3), increasing to 50% by the uppermost Main Body/Ramsey Ranch Member, where *Platycarya* foliage first occurs (Roehler, 1992b). *Platycarya* presence is provisionally taken as an indicator of warmth, and the increase in *Platycarya* abundance is interpreted as evidence for a warming trend. In the Bighorn Basin, *Platycarya* pollen abundance increases through the Willwood Formation from its FAD near the base to over 20% of palynomorphs at the first stratigraphic levels where the foliage is preserved (Wing and Hickey, 1984). In the study area, the *Hadrianus* FAD (Hutchison, 1980), another strong proxy for warm winters, occurs at about the same time as the first record of *Platycarya* pollen abundance (Fig. 5.2).

The megaflora from the Latham coal zone indicates warm, mild, and somewhat humid conditions, although the low diversity of the assemblage limits interpretation. Foliage of palms, *Zingiberopsis*, and *Platycarya* are all present, in addition to leaves of the tree fern *Cnemidaria* and the aquatic fern *Salvinia*, both known only from subtropical to tropical climates today. However, the dominance of "*Meliosma*" *longifolia* (55% of dicot specimens), a form known from the Tiffanian-Graybullian of northern Wyoming and North Dakota, makes it unlikely that Latham conditions were significantly warmer than in the Clarkforkian. Leaf-margin analysis indicates MAT of 16.4°C, similar to Clarkforkian temperatures, although this value is quite tentative because of the high sampling error (Fig. 5.4; Table 5.1).

Wet conditions are evident from fruits resembling sedge nutlets (Table 5.3), the presence of *Salvinia* and two other ferns, and the existence of the Latham coal itself, which reaches 6 m in thickness (Masursky, 1962). However, tectonically-induced waterlogging may have played a greater role than precipitation in maintaining moist habitats at this time of increasing topographic complexity. Leaf sizes are smaller than in the Clarkforkian despite the very fine-grained depositional environment, and leaf-area analysis, albeit from a small sample size, indicates MAP near 113 cm (Fig. 5.4). Small leaves in the Lysitean have also been observed qualitatively in the Bighorn Basin (S. Wing, pers. comm., 1997) and in an assemblage from the Regina Member of the San Jose Formation, San Juan Basin, New Mexico, first reported by Tidwell et al. (1981) and recently recollected (Wilf and Wing, field obs., 1997). This combination of evidence supports a somewhat drier regional climate in the Lysitean than in the Clarkforkian but with sufficient rainfall and runoff throughout the year in the study area to allow significant peat formation in the lowest areas of the Great Divide Basin.

The Sourdough assemblage unequivocally indicates hot and humid conditions. The influx of immigrant dicot families with tropical affinities and the continuing presence of palms, *Cnemidaria*, *Salvinia*, *Platycarya*, and *Zingiberopsis* provide strong floristic evidence for high temperatures. Leaf textures are more variable than in the Clarkforkian with thicker overall textures, a feature associated today with broad-leaved evergreen tropical forests. Preliminary observations on insect feeding damage to fossil leaves reveals that herbivory is more host specific than in the Paleocene, with a higher diversity of specialized mines. Modern tropical forests are considered to have more specialized insect damage than temperate forests because tropical species tend to have more elaborate chemical defenses, prohibiting generalized feeders (e.g., Coley and Aide, 1991). Leaf-margin analysis indicates MAT near 22.0°C (Fig. 5.4; Table 5.1).

The Sourdough environment was clearly wet. Coals are thick and dark, and claystones at some localities have fine laminae indicating deposition in standing water (e.g., USNM loc. 41332). Hydrophilic plants include a water lily (Nymphaeaceae sp.), horsetails, and eight species of ferns. High diversity of insect mines is associated in modern forests with humid conditions (Fernandes and Price, 1988). Many plant species are represented by large leaves, suggesting that the air was humid, and leaf-area analysis indicates MAP near 146 cm.

The megaflora from the Niland Tongue documents the continuation of warm conditions from Sourdough time. Eleven of the estimated 23 species in the Niland Tongue assemblage persisted from the Sourdough level (Table 5.3). Thermophilic plants include a palm (*Sabalites* sp.), *Platycarya castaneopsis*, *Salvinia*, and *Zingiberopsis.* Leaf-margin analysis of the 14 dicot species indicates MAT near 23.0°C (Fig. 5.4; Table 5.1). Several dicot forms have very small leaves despite the fine-grained environment of deposition, so that leaf-area analysis indicates MAP near 86.3 cm (Fig. 5.4; Table 5.1). This estimate is probably too low given (1) the small number of species recovered for analysis; (2) the floristic continuity from the Sourdough assemblage; (3) the presence of five species of ferns; (4) that Niland Tongue depositional environments were essentially identical to those of the Ramsey Ranch Member (Roehler, 1993); and (5) palynological data supporting abundant precipitation in the Niland Tongue (Nichols, 1987). Further evidence against drying is the immediately overlying Scheggs Bed of the Tipton Shale Member of the Green River Formation, which represents the first, short-lived expansion of Lake Gosiute to cover most of the Greater Green River Basin with fresh water (Roehler, 1993: Fig. 50). The Scheggs Bed gave way to a definitive and extended drying interval in the latest early Eocene, represented by the saline Rife Bed of the Tipton Shale Member, the evaporitic Wilkins Peak Member of the Green River Formation, and the heavily red bedded Cathedral Bluffs Tongue of the Wasatch Formation (e.g., Roehler, 1993).

The Wilkins Peak assemblage provides strong evidence for continued, but lessened warmth in the area in a more arid and seasonal climate. Foliar analysis indicates MAT near 18.8°C and MAP near 75.8 cm (Fig. 5.4; Table 5.1). Sufficient water was available to support occasional ferns, horsetails and *Ceratophyllum muricatum*, which inhabits shallow to ephemeral fresh water environments of tropical and subtropical regions today (Les, 1997), and to preserve delicate insect body fossils, an articulated shell of an unidentified turtle, and a ?clupeid fish skeleton. This evidence also indicates that the Little Mountain assemblage was derived from a more fresh and expanded stage of the Wilkins Peak lake cycle (Eugster and Hardie, 1975; Smoot, 1983).

Climatic overview

Summary results from leaf-margin and leaf-area analysis are shown in Figure 5.4. Also plotted for comparison are previously published leaf-margin data from the Bighorn and northern Wind River basins of northern Wyoming (Hickey, 1980; Wing et al., 1991, 1999).

The temperature curves are in accord on several important points. First, the southern Wyoming temperature means are consistently as warm or warmer than the north. Second, a warming trend appears within the late Paleocene, in agreement with deep-sea cores (Corfield and Cartlidge, 1992; Zachos et al., 1994). Third, the northern Wyoming data indicate cooling near 54 Ma followed by an abrupt warming trend to the early Lostcabinian; the southern Wyoming data corroborate the warming trend, although they are insufficient to determine to what extent cooling preceded the warming. Fourth, both data sets indicate maximum temperatures by the basal Lostcabinian, and the southern Wyoming data indicate that this peak continues into Niland Tongue time. This maximum corresponds to the Cenozoic thermal maximum known from ocean cores

(Miller et al., 1987; Zachos et al., 1994). Fifth, moderate cooling is indicated following this maximum, also in agreement with core data and recent work on the isotopic geochemistry of calcite cements found in late early to early middle Eocene fossil wood from Antarctica (Pirrie et al., 1998).

These results strongly support leaf-margin analysis as a robust methodology for inferring Paleogene continental paleotemperatures because of the strong agreement between leaf-margin and floristic, faunistic, and sedimentological data and the generally higher margin percentages in the South, despite a short latitudinal distance of 2-4°.

The paleoclimatic results differ somewhat from the climate curves published by Roehler (1993: 68) for the Eocene part of the section. Peak Eocene temperature and precipitation in this study occur in the middle early Eocene followed by cooling and drying in the late early Eocene (Fig. 5.3). Roehler's report also noted increasing temperature and precipitation in the middle early Eocene, to lower values near 16°C MAT and 110 cm MAP. However, Roehler placed the Eocene temperature and precipitation maximum in the early middle Eocene, during Laney time. This report did not cover the Laney Member, but the evidence presented here is that hot and humid climates already existed in parts of the late Paleocene and early Eocene.

Davies-Vollum and Wing (1998) noted the absence of tabular carbonaceous shales in the 350-600 m portion of the Willwood Formation, suggesting a regional drying trend from the early to the late early Eocene as a possible cause. Among other evidence, these authors cited (1) the transition from the lacustrine Luman Tongue of the Green River Formation to the fluvial Niland Tongue of the Wasatch Formation; and (2) the evaporitic nature of the Wilkins Peak Member of the Green River Formation. If the Sourdough coal is approximately the same age as the 621 m level of the Willwood Fm., then the 350-600 m portion of the Willwood Formation is older than all of the units listed above as well as the unequivocally humid Sourdough assemblage. The 350-600 m interval appears to correlate with the uppermost Main Body and lower Ramsey Ranch Member of the Wasatch Formation, another possible time of drying in the Greater Green River Basin separated from later drying by the wet Sourdough interval (Fig. 5.4). Early Eocene drying in the Rocky Mountains was not unidirectional but took place in several pulses and reversals.

While the Green River lake system may have had an ameliorating effect on the climate of southern Wyoming (Sloan, 1994), it is clear from this study that the ancient lakes were not a primary cause of the area's warm climates with minimal frost, which existed independent of lakes. Humid subtropical conditions were already present in the area in the Clarkforkian, when the lake system was confined to the Uinta Basin of Utah (e.g., Grande, 1984). Predominantly frost-free climate as indicated by the Latham assemblage predates the Lostcabinian Luman Tongue of the Green River Formation, the first appearance of Lake Gosiute, by about 200-300 ky. The Sourdough assemblage, from the Cenozoic thermal maximum, immediately underlies the Luman Tongue of the Green River Formation but still predates the Scheggs Bed of the Tipton Shale Member, the first major expansion of the lake, by approximately 1 my. The first appearance of the Colorado arm of Lake Uinta also did not occur until the Lostcabinian (Kihm, 1984). Finally, the only long-lived and fully expanded portion of Lake Gosiute was the middle Eocene Laney Member, which postdated the entire interval studied here.

DIVERSITY

Decreasing latitude is generally associated with higher plant diversity, which includes such properties as local species richness (alpha diversity), regional species richness (gamma diversity), variation in species composition across a landscape (beta diversity), and evenness (Whittaker, 1972; Thorington et al., 1982; Gentry, 1988; Crane and Lidgard, 1989; Schluter and Ricklefs, 1993; Tilman and Pacala, 1993; Latham and Ricklefs, 1993a, 1993b; Rosenzweig, 1995; Richards, 1996). Only the fossil record allows us to study changes in vegetational diversity in an extended time series. If temperature is an important control on diversity, and other controls such as moisture, topography and area are kept more or less constant, then the same trends seen with decreasing latitude in extant forests should be seen with increasing temperature in fossil forests as latitude is held constant. In an earlier study, Wing et al. (1995) found no strong relationship between diversity and paleotemperature in the Paleocene-Eocene of the Bighorn Basin, although revised estimates show much better correlation (Wing et al., 1999).

In the study area, topography can be assumed to have been uniform for all of the fluvial assemblages (all but Wilkins Peak). Although surrounding uplifts are thought to have been more active in the early Eocene than in the late Paleocene, plant fossil deposition only occurred in the flattest and lowest portions of basin centers. Moisture also appears to have been generally abundant (Fig. 5.4). The total area available for plant colonization remained similar.

Alpha diversity can be approximated by species richness at individual quarries. This measure shows little variation though time when only the mean is examined (Table 5.1). This result is not surprising because there appear to be general limits on the number of species that can be preserved, on average, in a single fluvial assemblage from a quarry of small spatial scale. In a recent survey, Wing and DiMichele (1995) found a mean of about ten species per quarry both for 116 Cenozoic and 35 Paleozoic fluvial compression assemblages. In the present study, there are a large number of low-diversity sites at all levels sampled, which may account for the lower mean. The high mean for Bison Basin, 11 species, is the exception.

Maximum richness per sample (Nmax in Table 5.1) is perhaps a more informative approximation of alpha diversity, as noisy, species-poor sites are eliminated. This figure was distinctly higher for the Lostcabinian Sourdough and Niland Tongue assemblages than for the Paleocene. Three Sourdough quarries were more rich (24, 21, and 17 species) than the most speciose Clarkforkian site (16 species).

One proxy for gamma diversity is the raw number of species recovered per sampling interval (Table 5.1), although this does not account directly for sampling intensity. However, the Sourdough assemblage yielded 54 species from 31 quarries in a small stratigraphic range, whereas the lumped Clarkforkian assemblage, from a longer total time interval, produced 46 species from 49 sites. By this basic measure, the Lostcabinian flora was far more species-rich than that of the cooler Clarkforkian.

Rarefaction provides another proxy for past gamma diversity. A bootstrapping procedure that randomly resamples quarries from the best sampled levels allows a direct comparison of species richness at equivalent sampling intensities (Fig. 5.5). The Sourdough assemblage is clearly more rich at any sampling intensity than “Clarkforkian lumped” or the Big Multi section (Fig. 5.5A). The Big Multi curve is unsurprisingly similar to “all Clarkforkian”, as the former is a large subset of the latter. The Bison Basin curve again shows more richness than Big Multi or “all Clarkforkian”, an unexpected result given that the climate was cooler (Fig. 5.4). Examination of standard deviations of the rarefaction means shows that the Sourdough level is significantly more diverse than the lumped Clarkforkian (Fig. 5.5B). The error bars separate at 13 quarries: the probability is less than 3% that if a random 13 quarries were collected, the Sourdough assemblage would erroneously appear less diverse than the Clarkforkian.

Qualitative examination of the Clarkforkian census data illustrates the homogenous and monodominant nature of this paleovegetation (Table 5.4). *Corylites* sp. was dominant at eight of the 10 censused quarries and comprised 62% of total leaves. The only exceptions were *Persites argutus* at USNM loc. 41287 and *Averrhoites affinis* at USNM loc. 41295. Other leaf types with high counts were “*Ampelopsis*” *acerifolia* and “*Cinnamomum*” *sezannense. Glyptostrobus europaeus* was not censused but was present at 53% of the Clarkforkian sites. These results are strikingly similar to those from the Tiffanian Bison Basin assemblage (Gemmill and Johnson, 1997). There, *Corylites*, also in co-occurrence with *Palaeocarpinus aspinosa*, was overwhelmingly dominant as well (38% of all leaves). “*Ampelopsis*” (*Archeampelos*) *acerifolia* was also a prominent component, as was *Metasequoia occidentalis*, a taxodiaceous conifer that may have occupied a similar niche to *Glyptostrobus*. While nearly all minor taxa from the Bison Basin were gone in the warmer Clarkforkian, the dominance structure was nearly unchanged. Similarly low diversity indices for the Bison Basin and Clarkforkian samples support these observations of homogeneity and concentrated dominance (Table 5.1).

Census data from the Sourdough assemblage show mixed dominance relative to the Tiffanian and Clarkforkian (Table 5.5). One or the other of two species, *Alnus* sp. and *Platycarya americana*, dominate most leaf counts, together accounting for about the same percentage of total leaves (59%) as did *Corylites* in the Clarkforkian. *Apocynaceae* sp., aff. *Sloanea*, “*Dombeya*” *novi-mundi*, and an undescribed dicot (RR48) are all significant in leaf counts. Most diversity indices from the Sourdough sample are higher than in the Tiffanian and Clarkforkian because of the presence of two major dominants and higher species richness in most of the censuses (Tables 5.1, 5.5).

Another way to examine vegetational heterogeneity is to compare frequency data. This approach allows the use of the full presence-absence matrix of all sites and species, rather than only dicot leaves at census sites. A frequency vs. rank frequency plot (Fig. 5.6) shows that in the Sourdough assemblage, no species occurs at more than about half of all sites, whereas several taxa each occur at a majority of sites in the late Paleocene. In this data set, the Bison Basin sample possesses the largest number of ubiquitous taxa, with several appearing at all ten quarries (Fig. 5.6). The combination of higher species frequency, site richness, and bootstrapped richness, and a more lacustrine setting at Bison Basin vs. the Clarkforkian assemblages favors a scenario of more spatial mixing of vegetation prior to deposition at Bison Basin, overprinting climatic effects on diversity (Figs. 5.5, 5.6; Table 5.1).

In summary, vegetational diversity did not change substantially from the Tiffanian to the Clarkforkian by most measures and may have decreased. Despite climatic warming and high species turnover, the dominant species were nearly identical throughout this interval. All measures of diversity definitively increased by the time of the Wasatchian thermal maximum. The overall pattern of relatively low Tiffanian and Clarkforkian diversity and high Wasatchian diversity is similar to that observed in faunal assemblages from the Bighorn Basin (Rose, 1981b).

These results raise several questions for future study. First, why did the overall structure of basin forests not change in the Clarkforkian, a time when temperatures were rising and a large number of thermophilic plants and animals arrived in the area? The Clarkforkian appears to be a time of major flux and migration, against a backdrop of global warming, without any fundamental ecological reorganization except for an increase in the dominance of a species already dominant in the Tiffanian, *Corylites* sp. This pattern from the past may be useful for understanding the response of modern temperate biota to climate change.

Second, what caused the final breakdown of the homogenous forest structure of the late Paleocene and the turnover of most plant species? Early Eocene cooling near 54 Ma as suggested by Wing et al. (1999) brought estimated MAT back to Tiffanian values (Fig. 5.4). However, many of the dominant Clarkforkian species had persisted from the Tiffanian and presumably were still tolerant of such temperatures. Changes in regional rainfall patterns, in combination with the cooling, may have played a major role. Both the Tiffanian and the Clarkforkian were humid, while there is sedimentary evidence from the Bighorn Basin and leaf-area evidence from this study that indicate drying shortly after the time of possible cooling (Davies-Vollum and Wing, 1998; Fig. 5.4; Table 5.1).

CONCLUSIONS

The Greater Green River Basin of southwestern Wyoming contains an outstanding late Paleocene-early Eocene megafloral record that I have used to analyze changes in paleoclimate, paleoecology, and floristic composition. Late Paleocene estimated mean annual temperature increased from about 13°C in the Tiffanian to nearly 20°C within the early Clarkforkian. Humid conditions prevailed, with annual rainfall near 150 cm. Mild climates continued in the Graybullian, although some cooling and drying may have taken place. Temperatures warmed again from the late Graybullian to the early Lostcabinian, and humid conditions returned. Early Lostcabinian mean annual temperatures were near 22°C and mean annual precipitation was again near 150 cm. Warm temperatures persisted in the later Lostcabinian and then dropped slightly in the earliest Bridgerian to about 19°C, as annual rainfall decreased sharply to approximately 75 cm in a more seasonal and arid climate. Generally frost-free conditions were present throughout the study interval, with the exception of the Tiffanian and possibly parts of the Graybullian. The Green River lake system was not a primary cause of mild Eocene winters in southern Wyoming because the lake system was not present or not well developed during several warm intervals.

The vegetational response to these climate changes was strongly pronounced. There were two turnover events that each involved the first and last appearances of over 80% of species. The first accompanied the late Graybullian to Lostcabinian warming trend, and the second coincided with Wasatchian-Bridgerian drying. Major immigrations of families with modern tropical affinities occurred with Clarkforkian as well as Wasatchian warming, although most families of plants known to be present in the late Paleocene persisted throughout the study interval. In similar depositional settings, early Eocene plant assemblages show greater diversity than in the late Paleocene. As warm temperatures were also present in the Clarkforkian, the relative lack of diversity at that time despite the influx of thermophilic taxa is puzzling and may reflect the persistence of "temperate" community dynamics.

These results both complement and closely track the Bighorn Basin record at current levels of resolution. Similar climatic and biotic events have now been observed at all latitudes of Wyoming, showing that they are regional and not local in extent and increasing their value for understanding terrestrial events during the Paleocene-Eocene interval.

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TABLE 5.1. SAMPLING, PALEOCLIMATIC, AND DIVERSITY DATA

Level	BB	Cf	Mu	WM	La	Sd	NT	WP	Total
#Quarries	10	49	15	6	7	31	5	4	120
#Morphotypes	28	55	34	14	19	66	24	54	203
#Species	28	46	28	12	17	54	23	40	167
#Dicots	24	36	20	9	12	41	14	32	
P	0.375	0.444	0.600	_	0.500	0.683	0.714	0.578	
LMAT,°C	12.6	14.7	19.5	_	16.4	22.0	23.0	18.8	
σ(LMAT),°C	3.0	2.5	3.4	_	4.4	2.2	3.7	2.7	
MlnA	_	7.64	7.58	_	7.23	7.70	6.73	6.50	
LMAP,cm	_	142	137	_	113	146	86.3	75.8	
se+(LMAP),cm	_	61.2	59.2	_	48.9	63.2	37.3	32.7	
se-(LMAP),cm	_	42.7	41.4	_	34.2	44.1	26	22.9	
Nmean	11	5.0	6.3	2.8	4.4	6.3	6.0	21	
Ndev	2.3	3.3	3.8	1.5	3.4	5.4	6.6	9.9	
Nmax	14	16	14	5.0	12	24	17	32	
Dmean	0.48	0.25	0.34	_	_	0.45	_	_	
Dmax	0.57	0.60	0.60	_	_	0.73	_	_	
Dcum	0.56	0.59	0.50	_	0.66	0.80	_	_	
H'mean	0.88	0.51	0.62	_	_	1.0	_	_	
H'max	1.1	1.1	1.1	_	_	1.7	_	_	
H'cum	1.0	1.3	1.1	_	1.5	2.1	_	_	

Notes: Sampling intervals: (1) BB = Bison Basin, Fort Union Formation; (2) Cf = lumped Clarkforkian, Fort Union Fm.; (3) Mu, Big Multi local section, Fort Union Fm.; (4) WM: Main Body of Wasatch Fm.; (5) La: Latham coal zone, Ramsey Ranch member of Wasatch Fm.; (6) Sd, Sourdough and Monument coal zones, Ramsey Ranch member of Wasatch Fm.; (7) NT: Niland Tongue of Wasatch Fm.; (8) WP: Wilkins Peak Member of Green River Fm. Total number of quarries includes six depauperate sites in the Ramsey Ranch Member that were not in the Great Divide Basin and one from the Luman Tongue of the Green River Fm. (Fig. 5.1); these were excluded from further analysis. Estimated total number of species = #leaf types (165) – 1 for "leaf rosette" (Table 5.3) + 1 each for *Equisetum*, *Ceratophyllum*, and "*Sparganium*". Most reproductive types were not counted because of the possibility that they are parts of the same plants that produced leaves. #Dicots = number of woody dicots used for paleoclimate analyses. *P* = proportion of entire-margined woody dicots. LMAT = estimated mean annual temperature from leaf-margin analysis; σ(LMAT) = sampling error on the MAT estimate (Wilf, 1997: Eq. 4). MlnA = mean natural log leaf area; LMAP = estimated mean annual precipitation from leaf-area analysis; se+ = standard error in positive direction; se- = standard error in negative direction (see Wilf et al., 1998). N = number of species. D = Simpson's Index; H' = Shannon-Wiener Index, formulae as in Wilf et al. (1998); these indices for Bison Basin were recalculated for compatibility from Gemmill and Johnson's (1997) data to exclude non-dicots. Subscripts: "mean" = mean value; "dev" = one standard deviation; "max" = maximum value; "cum" = all quarries in sample combined; "_" = data not available or not applicable.

TABLE 5.2. INFERRED DEPOSITIONAL ENVIRONMENTS BASED ON LITHOLOGIES OF FOSSILIFEROUS BEDS*

Lithology	Paleoenvironment
Claystone, poorly laminated	Distal floodplain swamp
Carbonaceous shale	Distal floodplain swamp or oxbow[†]
Carbonaceous siltstone	Distal floodplain, infilling swamp
Fine-grained sandstone	Proximal to channel (fluvial deposits) or shallow lake-margin (Wilkins Peak only)
Medium-grained sandstone	Channel

*Lithologic data for each locality given in Appendix 5.1.

[†] The carbonaceous shales in the Fort Union Formation and the Ramsey Ranch Member and Niland Tongue of the Wasatch Fm. are conformable with underlying units and tabular when traceable, interpreted as swamp deposits using the criteria of Wing (1984). The carbonaceous beds in the Main Body of the Wasatch Fm. are limited in areal extent and appear to be oxbow deposits.

TABLE 5.3. PRELIMINARY SYSTEMATIC LIST OF THE FLORA, SHOWING DISTRIBUTION OF EACH TAXON WITHIN THE EIGHT MAJOR SAMPLING LEVELS AND KNOWN RANGE ELSEWHERE

Species or morphotype (Morphotype no.; reference specimen no.)	Organ	BB	Cf	Mu	WM	La	Sd	NT	WP
Sphenopsida									
Equisetaceae									
Equisetum sp. (FW21;7978)	A	X	X	X	_	_	X	_	X
Polypodiopsida									
Blechnaceae									
Woodwardia gravida Hickey (FW19-47;7979)	F	_	X	X	_	_	X	_	_
Cyatheaceae									
Cnemidaria magna Hickey (RR22;7980)	F	_	_	_	_	X	X	_	_
Dryopteridaceae?									
“Tatman fern” (RR21;7988)	F	_	_	_	_	_	X	_	_
Polypodiaceae?									
Allantodiopsis erosa Lesquereux (RR32;7981)	F	_	X	X	_	_	X	_	_
"*Allantodiopsis* sp. 2" (RR35;7982)	F	_	_	_	_	_	X	_	_
Pteridaceae									
Acrostichum hesperium Newberry (RR80;7983)	F	_	_	_	_	_	_	X	_
Salviniaceae									
Salvinia preauriculata Berry (RR06;7984)	F	_	_	_	_	X	X	X	_
Schizaeaceae									
Lygodium kaulfussi Heer (RR07;7985,7986)	F	_	_	_	_	X	X	X	_
Thelypteridaceae?									
Thelypteris iddingsi (Knowlton) MacGinitie (RR69;7987)	F	_	_	_	_	_	X	X	_
Incertae sedis									
(RR51;7989)	F	_	_	_	_	_	_	X	_
(GR553;UF15882-7376)	F	_	_	_	_	_	_	_	X
Cycadopsida									
Cycadaceae									
Cycad leaf (FW52;7991)	F	_	X	_	_	_	_	_	_
? (FW26;7992)	F	_	X	_	_	_	_	_	_
? (RR68;7990)	F	_	_	_	_	_	_	X	_
Pinopsida									
Pinaceae									
Pinus sp. (5-needled) (GR542;7993)	F	_	_	_	_	_	_	_	X
Pinaceae sp. (GR543;UCMP153121)	Fr	_	_	_	_	_	_	_	X
Taxodiaceae									
Glyptostrobus europaeus (Brogniart) Heer (FW20;7994)	F,C	_	X	X	_	_	X	_	X
Metasequoia occidentalis Newberry (FW04,FW15;7995,7996)	F,C	X	X	X	X	_	_	_	_
Liliopsida									
Arecaceae		_	_	_	_	_	_	_	_
Sabalites/Amesoneuron (RR34;7998)	F	_	X	X	_	X	X	X	X
Cyperaceae?									
sedge-like fruits (RR53;7999)	Fr	_	_	_	_	X	_	_	_
Smilacaceae?									

Species or morphotype (Morphotype no.; reference specimen no.)	Organ	BB	Cf	Mu	WM	La	Sd	NT	WP
aff. *Smilax* (GR550;UF15882-20791)	F	_	_	_	_	_	_	_	X
Sparganiaceae?									
"*Sparganium*" *stygium* Heer (RR91;8000)	Fr	_	_	_	_	_	X	_	_
Zingiberaceae									
Zingiberopsis isonervosa Hickey (RR03;8001)	F	_	X	X	X	X	X	X	_
Incertae sedis									
Monocot A (RR86;7997)	F	_	_	_	_	_	_	X	_
Monocot B (GR513;UF15882-20793)	F	_	_	_	_	_	_	_	X
Magnoliopsida									
Aceraceae									
Dipteronia sp. (GR551;UF15882-7383')	Fr	_	_	_	_	_	_	_	X
Anacardiaceae									
Rhus nigricans (Lesquereux) Knowlton (GR529;8004)	F	_	_	_	_	_	_	_	X
Apocynaceae									
Apocynaceae sp. of Wing 1998 (RR17;8005)	F	_	_	_	_	X	X	_	_
Araliaceae?									
aff. *Dendropanax latens* MacGinitie (RR60;8006)	F	_	_	_	_	_	X	X	_
Betulaceae									
Alnus sp. (RR14;8007)	F	_	_	_	_	X	X	X	X
Alnus sp. female cones (RR14a;8008)	C	_	_	_	_	_	X	_	_
? *Alnus?* catkins (RR90;8009)	I	_	_	_	_	_	X	_	_
Corylites sp. (Betulaceae sp. 1 of Wing 1998) (FW01;8010)	F	X	X	X	X	_	_	_	_
Palaeocarpinus aspinosa Manchester and Chen (FW16;8011)	Fr	X	X	X	_	_	_	_	_
Betulaceae sp. catkin (FW67;8012)	I	_	X	_	_	_	_	_	_
Caprifoliaceae?									
"*Viburnum*" *antiquum* (Newberry) Hollick (FW43;8014)	F	_	X	_	_	_	_	_	_
"*Viburnum*" *asperum* Newberry (FW39;8013)	F	X	X	_	_	_	_	_	_
Ceratophyllaceae									
Ceratophyllum muricatum Cham. subsp. incertum (Berry) Herendeen, Les, and Dilcher (GR516;UF15882-7455')	Fr	_	_	_	_	_	_	_	X
Cercidiphyllaceae									
Cercidiphyllum genetrix (Newberry) Hickey (FW51;8015)	F	_	X	_	_	_	_	_	_
Joffrea sp. (spp?) (FW50;8016)	Fr	X	X	_	_	_	_	_	_
? aff. Cercidiphyllaceae (FW09;8017)	F	_	X	X	_	_	_	_	_
Cornaceae									
Cornus hyperborea Heer (FW34;8018)	F	_	X	X	_	_	_	_	_
"*Viburnum*" *cupanioides* (Newberry) Brown (FW44;8019)	F	X	X	_	_	_	_	_	_
Elaeocarpaceae?									
aff. *Sloanea* (Divot XXV of Wing 1998) (RR18;8020)	F	_	_	_	_	_	X	_	_
Euphorbiaceae									
aff. *Alchornea* (GR546;UCMP153135)	F	_	_	_	_	_	_	_	X

TABLE 5.3

Species or morphotype (Morphotype no.; reference specimen no.)	Organ	BB	Cf	Mu	WM	La	Sd	NT	WP
Stillingia casca Hickey (RR47;8021)	F	_	_	_	_	X	X	_	_
Fagaceae									
Fagaceae sp. (GR522; UF15882-7405)	F	_	_	_	_	_	_	_	X
Hamamelidaceae									
"*Acer*" (*Liquidambar*) *lesquereuxi* Knowlton (GR545;UCMP153007)	F	_	_	_	_	_	_	_	X
Hippocastanaceae									
Aesculus sp. (FW63;DMNH15273)	F	_	X	_	_	_	_	_	_
Juglandaceae									
"*Carya*" *antiquorum* Newberry (FW30;8022)	F	_	X	X	X	_	_	_	_
Palaeocarya clarnensis Manchester (GR531;UF15882-7359)	Fr	_	_	_	_	_	_	_	X
Platycarya americana Hickey (RR01;8023)	F	_	_	_	_	X	X	_	_
Platycarya americana Hickey (RR70;8024)	Fr	_	_	_	_	_	X	_	_
Platycarya americana Hickey, pistillate (RR02;8025)	I	_	_	_	_	_	X	_	_
? *Platycarya americana* Hickey, staminate? (RR75;8026)	I	_	_	_	_	_	X	_	_
Platycarya castaneopsis Wing and Hickey (RR09;8027)	F	_	_	_	_	_	_	X	_
Platycarya castaneopsis Wing and Hickey (RR16;8028)	Fr	_	_	_	_	_	_	X	_
Pterocarya macginitii Manchester and Dilcher (GR532;UF15882-7457')	Fr	_	_	_	_	_	_	_	X
Lauraceae									
aff. *Cinnamomum* (RR19;8030)	F	_	_	_	_	_	X	_	_
"*Cinnamomum*" *sezannense* (FW02;8031)	F	_	X	X	_	_	_	_	_
? "*Ficus*" *planicostata* Lesquereux (FW54;8037)	F	_	X	_	_	_	_	_	_
aff. *Ocotea* (FW03;8032)	F	_	X	X	_	_	_	_	_
aff. *Ocotea* sp. 2 (GR521;8033)	F	_	_	_	_	_	_	_	X
*Persites argutu*s Hickey (FW08,WM10;8036)	F	_	X	X	_	_	_	_	_
Lauraceae sp. (FW28;8035)	F	_	X	_	_	_	_	_	_
Lauraceae sp. 2 (RR46;8034)	F	_	_	_	_	X	X	_	_
Leguminosae									
Caesalpinia flumen-viridensis Herendeen and Dilcher (GR534;UF15882-7388)	Fr	_	_	_	_	_	_	_	X
aff. *Gleditsia* (RR29;8039)	F	_	_	_	_	_	_	X	_
"*Gymnocladus*" *hesperia* (Brown) MacGinitie (GR515;UCMP153137)	F	_	_	_	_	_	_	_	X
Leguminosites lesquereuxiana (Knowlton) Brown (GR517;UCMP153134)	F	_	_	_	_	_	_	_	X
Parvileguminophyllum coloradensis (Knowlton) Call and Dilcher (GR520;8040)	F	_	_	_	_	_	_	_	X
Leguminosae sp. (GR501;UF15882-7367)	F	_	_	_	_	_	_	_	X
Magnoliaceae									
Magnoliaceae sp. (FW07-22-46;8041)	F	_	X	X	_	_	_	_	_
Magnoliaceae sp. 2 (RR36;8042)	F	_	_	_	_	_	X	_	_
? Magnoliales sp. (RR12;8038)	F	_	_	_	_	_	X	_	_
Malvaceae-Sterculiaceae-Bombacaceae									
"*Dombeya*" *novi-mundi* Hickey (RR05;8044)	F	_	_	_	_	X	X	X	_
Malvales aff. *Kydia* (FW61;DMNH15279)	F	_	X	_	_	_	_	_	_

TABLE 5.3

	Species or morphotype (Morphotype no.; reference specimen no.)	Organ	BB	Cf	Mu	WM	La	Sd	NT	WP
	Menispermaceae									
	aff. *Abuta* (GR507;UF15882-20788)	F	_	_	_	_	_	_	_	X
	aff. *Atriaecarpum clarnense* Manchester (RR56;8045)	Fr	_	_	_	_	_	X	_	_
?	aff. *Triclisia* (RR72;8047)	F	_	_	_	_	_	X	_	_
?	aff. Menispermaceae (RR63;8046)	F	_	_	_	_	_	X	_	_
	Myrtaceae									
	"*Eugenia*" *americana* (Lesquereux) MacGinitie (RR23;8048)	F	_	_	_	_	_	X	_	X
	Paleomyrtinaea sp. Pigg, Stockey, and Maxwell (FW66;8049)	Fr	_	X	X	_	_	_	_	_
	Nymphaeaceae									
	Nymphaeaceae sp. (RR43;8051)	F	_	_	_	_	_	X	_	_
	Olacaceae?									
	aff. *Schoepfia republicensis* (LaMotte) Wolfe and Wehr (RR44;8052)	F	_	_	_	_	_	X	X	_
	Oleaceae									
	Fraxinus sp. (GR535;UF15882-20575)	Fr	_	_	_	_	_	_	_	X
	Platanaceae									
?	"*Ficus postartocarpoides*" (FW06;8056)	F	_	(X)	X	_	_	_	_	_
	Macginitiea gracilis (Lesquereux) Wolfe and Wehr (FW48,RR25;8054)	F	_	X	_	_	_	X	_	_
	Macginitiea cf. *wyomingensis* (Knowlton and Cockerell) Manchester (GR518;UCMP153146)	F	_	_	_	_	_	_	_	X
	Platanus sp. (GR552;UF15882-7362)	Fr	_	_	_	_	_	_	_	X
	aff. *Platanus raynoldsi* Newberry (GR506;UF15882-21183)	F	X	_	_	_	_	_	_	X
	Proteaceae?									
	Proteaciphyllum minutum MacGinitie (RR84,GR527;8057)	F?	_	_	_	_	_	_	X	X
	Rhamnaceae									
	Hovenia sp. (RR15;8084)	F	_	_	_	_	_	X	_	_
	Salicaceae									
	aff. *Populus* (FW60;UF18126-13262)	F	_	X	_	_	_	_	_	_
	Populus cinnamomoides (Lesquereux) MacGinitie (GR528;8058)	F	_	_	_	_	_	_	_	X
	Populus wyomingiana (Berry) MacGinitie (RR62;8059)	F	_	_	_	_	_	X	X	_
	cf. *Salix cockerelli* Brown (GR524;8060)	F	_	_	_	_	_	_	_	X
	Sapindaceae									
	Allophylus flexifolia (Lesquereux) MacGinitie (GR547;UF15882-7441)	F	_	_	_	_	_	_	_	X
	Cardiospermum coloradensis (Knowlton) MacGinitie (GR511;8061)	F	_	_	_	_	_	_	_	X
	Koelreuteria viridifluminis (Hollick) Brown (GR530;UCMP153080)	Fr	_	_	_	_	_	_	_	X
?	aff. Sapindaceae (GR525;8062)	F	_	_	_	_	_	_	_	X
?	aff. Sapindaceae sp. 2 (Dicot XXXI of Wing 1998) (RR59;8063)	F	_	_	_	_	_	X	_	_
	Simaroubaceae									

Species or morphotype (Morphotype no.; reference specimen no.)	Organ	BB	Cf	Mu	WM	La	Sd	NT	WP
Ailanthus lesquereuxi Cockerell (GR533;UF15882-7382)	Fr	_	_	_	_	_	_	_	X
Theaceae									
Ternstroemites aureavallis Hickey (FW29;8064)	F	_	X	_	_	_	_	_	_
? aff. Theaceae (FW49;UF18126-13239)	F	_	X	_	_	_	_	_	_
? aff. Theaceae sp. 2 (FW57;DMNH15277)	F	_	X	_	_	_	_	_	_
Ulmaceae									
Cedrelospermum nervosum (Newberry) Manchester (GR512;UCMP153099)	F	_	_	_	_	_	_	_	X
Celtis sp.*	Fr	_	_	_	X	_	_	_	_
? "*Celtis*" *peracuminata* Brown (FW59;DMNH15271)	F	_	X	_	_	_	_	_	_
Chaetoptelea microphylla (Newberry) Hickey (RR50;8066)	F	_	_	_	_	_	X	_	_
Vitaceae?									
"*Ampelopsis*" *acerifolia* Newberry (FW14;8067)	F	X	X	X	_	_	_	_	_
Incertae sedis									
"*Astronium*" *truncatum* (Lesquereux) MacGinitie (GR556;UF20226)	I	_	_	_	_	_	_	_	X
Averrhoites affinis (Newberry) Hickey (RR41;8053)	F	_	X	X	X	X	X	X	X
Calycites sp. (5 sepals) (RR58;8071)	I	_	_	_	_	_	X	_	_
Calycites sp. (6 sepals) (RR71;8002)	I	_	(X)	X	_	_	X	_	_
"*Eucommia*" *serrata* (Newberry) Brown (FW45;8070)	F	_	X	_	_	_	_	_	_
"*Meliosma*" *longifolia* (Heer) Hickey (RR52;8003)	F	_	_	_	_	X	_	_	_
aff. *"Pterocarya" roanensis* MacGinitie (GR504;UF15882-7443)	F	_	_	_	_	_	_	_	X
aff. "*Viburnum*" *antiquum* (FW40;8069)	F	_	_	X	_	_	_	_	_
Dicot XXXVI of Wing 1998(RR48;8096)	F	_	_	_	_	_	X	_	_
Dicot XXXVII of Wing 1998 (RR27;8088)	F	_	_	_	_	_	X	_	_
(FW05;8072)	F	_	(X)	X	_	_	_	_	_
(FW18;8073)	F	_	(X)	X	_	_	_	_	_
(FW23;8074)	F	_	(X)	X	_	_	_	_	_
(FW24;8075)	F	_	X	X	_	_	_	_	_
(FW25;8076)	F	_	X	X	_	_	_	_	_
(FW27;8077)	F	_	X	X	_	_	_	_	_
?aquatic herb (FW31;8068)	F	_	_	X	_	_	_	_	_
(FW32;8078)	F	_	X	_	_	_	_	_	_
(FW55;8081)	I	_	X	_	_	_	_	_	_
herbaceous leaf rosette (FW58;8080)	F?	_	(X)	X	_	_	_	_	_
(FW62;DMNH15282)	F	_	X	_	_	_	_	_	_
fertile catkin (FW65;8055)	Fr	_	(X)	X	_	_	_	_	_
(FW68;8079)	F	_	(X)	X	_	_	_	_	_
(GR502;8120)	F	_	_	_	_	_	_	_	X
(GR503;8121)	F	_	_	_	_	_	_	_	X
(GR505;UF15882-26201)	F	_	_	_	_	_	_	_	X

Species or morphotype (Morphotype no.; reference specimen no.)	Organ	BB	Cf	Mu	WM	La	Sd	NT	WP
(GR508;UF15882-7430)	F	_	_	_	_	_	_	_	X
(GR509;UF15882-7408')	F	_	_	_	_	_	_	_	X
winged fruit (GR523;UF15882-7481)	Fr	_	_	_	_	_	_	_	X
(GR526;8122)	F	_	_	_	_	_	_	_	X
(GR536;8124)	Fr	_	_	_	_	_	_	_	X
bract with anastomosing veins (GR538;8125)	I	_	_	_	_	_	_	_	X
fruit w/ 2 epigynous wings (GR539;UCMP153003)	Fr	_	_	_	_	_	_	_	X
(GR549;UF15882-7415)	F	_	_	_	_	_	_	_	X
(GR554;UF15882-7411)	F	_	_	_	_	_	_	_	X
(GR555;8123)	F	_	_	_	_	_	_	_	X
(RR04;8082)	F	_	_	_	_	X	_	_	_
(RR10;8065)	F	_	_	_	_	_	X	_	_
(RR11;8127)	Fr	_	_	_	_	X	_	_	_
(RR13;8083)	F	_	_	_	_	_	X	_	_
(RR20;8085)	F	_	_	_	_	_	X	_	_
(RR24;8086)	F	_	_	_	_	_	X	_	_
(RR26;8087)	F	_	_	_	_	_	X	_	_
(RR31;8090)	F	_	_	_	_	_	X	_	_
(RR37;8091)	F	_	_	_	_	_	X	_	_
(RR38;8092)	F	_	_	_	_	_	X	_	_
(RR40;8093)	F	_	_	_	_	_	X	_	_
(RR42;8094)	F	_	_	_	_	_	X	_	_
(RR45;8095)	F	_	_	_	_	_	X	_	_
(RR49;8097)	F	_	_	_	_	_	_	X	_
(RR54;8098)	F	_	_	_	_	X	_	_	_
(RR55;8099)	F	_	_	_	_	_	_	X	_
(RR57;8100)	F	_	_	_	_	_	X	_	_
(RR64;8101)	F	_	_	_	_	_	X	_	_
(RR65;8102)	F	_	_	_	_	_	X	_	_
(RR66;8103)	F	_	_	_	_	_	X	_	_
(RR67;8104)	F	_	_	_	_	_	X	_	_
(RR73;8105)	F	_	_	_	_	_	X	_	_
(RR74;8106)	F	_	_	_	_	_	X	_	_
(RR78;8108)	F	_	_	_	_	X	_	_	_
(RR79;8109)	F	_	_	_	_	X	_	_	_
(RR82;8111)	F	_	_	_	_	_	_	X	_
(RR83;8112)	F	_	_	_	_	_	_	X	_
(RR85;8113)	F	_	_	_	_	_	_	X	_
(RR87;8114)	Fr	_	_	_	_	_	X	_	_
(RR89;8115)	Fr	_	_	_	_	_	X	_	_
(WM04;8116)	F	_	_	_	X	_	_	_	_
(WM16;8118)	F	_	_	_	X	_	_	_	_
(WM21;8029)	F	_	_	_	X	_	_	_	_

Notes: Light gray shading indicates range in Bighorn Basin at current level of correlational resolution after Wing (1998) as follows: Tiffanian of Bighorn Basin to BB; Clarkforkian to Cf and Mu; lower and upper *Haplomylus-Ectocion* Zones and *Bunophorus* Interval-Zone to WM; Lysitean to La; Lostcabinian to Sd and NT. Dark gray shading indicates that the species or a highly similar, possibly conspecific species is known from Bridgerian or younger strata anywhere in Rocky Mountains other than field area, from Wing (1998) and other sources. Organs: A, axis; F, foliage; C, cone; Fr, fruit/seed; I, part of inflorescence. "?" at left of row = tentative assignment to family; “aff.” = strong morphological similarity; quotes around a published genus name indicate likely incorrect assignment. Morphotype numbers are grouped lithostratigraphically: FW = Fort Union Fm; WM = Main Body of Wasatch Fm; RR = Ramsey Ranch Member and Niland Tongue of Wasatch Fm; GR = Green River Fm. If a morphotype appears in more than one of the preceding, it receives more than one morphotype number; however, only the morphotype number of the reference specimen is shown. Catalogue numbers of reference specimens: for USNM specimens, only the last four digits are shown, and the first two are “49”; e.g., “7978” indicates USNM 497978; complete catalogue numbers are shown for reference specimens from other institutions. Abbreviations for sampling levels as in Table 1. Only Bison Basin taxa that persist into younger levels are shown; see Gemmill and Johnson (1997) for a complete list. Parentheses about “Cf” entries indicates Clarkforkian taxon only found in Big Multi local section. Assignment of “*Viburnum*” *cupanioides* to Cornaceae from evidence compiled by S. R. Manchester (pers. comm. 1997). Plant fossils from the Luman Tongue of the Green River Formation (USNM loc. 41367) are not identifiable, consisting of ?nymphaeaceous rhizomes and indeterminate leaves.

**Celtis* sp. seeds are reported from the Main Body of the Wasatch Fm. by Roehler (1979) but were not collected in this study and are not included in the totals in Table 1.

TABLE 5.4. DICOT LEAF CENSUS COUNTS AND DIVERSITY INDICES: CLARKFORKIAN

Leaf type	USNM locality no. 41-										Cum	*f*
	281	287	293	295	300	301	263	265	270	272		
"*Ampelopsis*" *acerifolia*	0	5	0	0	2	0	0	6	269	11	8.5%	5
Averrhoites affinis	0	0	0	188	1	4	0	0	0	0	5.6%	3
"*Carya*" *antiquorum*	14	0	0	6	10	0	0	0	1	0	0.89%	4
aff. Cercidiphyllaceae	0	0	0	0	1	0	7	0	0	0	<0.5%	2
"*Cinnamomum*" *sezannense*	0	0	0	0	0	0	109	0	0	0	3.1%	1
Cornus hyperborea	0	17	0	0	0	0	0	0	13	0	0.87%	2
Corylites sp.	281	0	137	2	388	262	180	274	284	327	62%	9
Magnoliaceae sp.	0	0	0	0	14	0	0	0	19	0	0.95%	2
aff. *Ocotea*	0	16	3	1	44	0	0	0	12	22	2.8%	6
Persites argutus	0	411	0	17	26	37	2	0	22	3	15%	7
Ternstroemites aureavallis	0	0	0	14	0	0	0	0	0	0	<0.5%	1
aff. "*Viburnum*" *antiquum* (FW40)	0	0	0	0	0	0	0	0	2	0	<0.5%	1
FW18	0	0	0	0	0	0	0	0	0	1	<0.5%	1
FW25	0	0	0	0	0	0	0	1	0	0	<0.5%	1
FW27	0	0	0	0	1	0	0	0	0	0	<0.5%	1
#Leaf types	2	4	2	6	9	3	4	3	8	5	15	
#Leaves	295	449	140	228	487	303	298	281	622	364	3467	
Simpson's	0.091	0.16	0.042	0.31	0.35	0.24	0.50	0.049	0.60	0.19	0.59	
Shannon	0.19	0.37	0.10	0.69	0.80	0.44	0.79	0.13	1.1	0.43	1.3	

Notes: Data from quarries 253, 265, 270, 272 as in Wilf et al. (in press). "Cum" = cumulative data; "*f*" = frequency.

TABLE 5.5. DICOT LEAF CENSUS COUNTS AND DIVERSITY INDICES: SOURDOUGH ASSEMBLAGE (EARLY LOSTCABINIAN)

Leaf type	USNM locality 41-					Cum	*f*
	332	336	341	342	352		
Alnus sp.	2	374	0	175	64	33%	4
Apocynaceae sp.	0	0	0	13	201	11%	2
Averrhoites affinis	0	16	0	0	0	0.85%	1
Chaetoptelea microphylla	0	0	17	0	0	0.91%	1
aff. *Cinnamomum*	0	0	3	9	2	0.75%	3
"*Dombeya*" *novi-mundi*	0	0	0	79	5	4.5%	2
Hovenia sp.	0	0	0	8	41	2.6%	2
Magnoliales sp.	0	0	0	10	0	0.53%	1
Magnoliaceae sp. 2	0	0	0	0	5	<0.50%	1
Lauraceae sp. 2	0	0	129	0	0	6.95%	1
Platycarya americana	342	9	131	10	0	26%	4
Populus wyomingiana	1	0	2	0	11	0.75%	3
aff. Sapindaceae sp. 2	0	0	0	1	18	1.0%	2
aff. *Sloanea*	0	0	1	65	1	3.6%	3
Stillingia casca	0	0	13	0	0	0.69%	1
aff. *Triclisia*	0	0	0	0	1	<0.50%	1
RR20	0	0	0	17	0	0.91%	1
RR31	0	0	0	0	6	<0.5%	1
RR37	0	0	0	5	1	<0.5%	2
RR38	0	0	0	2	0	<0.5%	1
RR40	0	4	18	0	0	1.2%	2
RR48	0	0	60	0	0	3.2%	1
RR57	0	0	0	1	0	<0.5%	1
RR64	0	0	0	0	1	<0.5%	1
RR65	0	0	0	0	1	<0.5%	1
RR66	0	0	0	0	1	<0.5%	1
RR67	0	0	1	0	0	<0.5%	1
#Leaf types	3	4	10	13	15	27	
#Leaves	345	403	375	395	359	1877	
Simpson	0.017	0.14	0.73	0.73	0.64	0.80	
Shannon	0.056	0.33	1.5	1.7	1.4	2.1	

Notes: "Cum" = cumulative data; "*f*" = frequency.

APPENDIX 5.1. LOCALITY DATA

USNM loc. 41- (field no.)	Latitude (N)	Longitude (W)	NALMA	USGS Quadrangle	Comment
Fort Union Fm., inferred or known Clarkforkian: Washakie and Green River Basins					
252(9518)*	413239	1091547	Cf	Rock Springs 30' X 60'	badlands along Little Bitter Creek
254(9536)†	413301	1091534	Cf	“	“
255(9537)†	413257	1091548	Cf	“	“
256(9538)†	410950	1085511	Cf	“	“
257(9411)†	413046	1083845	Cf	Black Buttes 7.5'	near Union Pacific tracks
258(9520)§	413108	1083726	Cf	Bitter Creek 7.5'	“
259(9521)†	413106	1083721	Cf	“	“
260(9522)†	413055	1083705	Cf	“	“
261(9525)§	413108	1083726	Cf	“	“
262(9412)§	413347	1083455	Cf	“	immediately above Big Multi
263(9413)§	413347	1083455	Cf	“	“
264(9414)§	413349	1083448	Cf	“	4 m above Big Multi
265(9415)*	413348	1083432	Cf	“	18 m above Big Multi
266(9416)†	413353	1083433	Cf	“	“
267(9417)†	413357	1083433	Cf	“	“
268(9432)§	413338	1083424	Cf	“	“
269(9433)§	413330	1083431	Cf	“	“
270(956)†	413357	1083433	Cf	“	“
271(9523)*	413403	1083437	Cf	“	“
272(9524;9614)*†	413407	1083431	Cf	“	“
273(9530)*	413324	1083444	Cf	“	“
274(961)*†	413357	1083433	Cf	“	“
275(962)#	413406	1083445	Cf	“	11 m above Big Multi
276(963)†	413355	1083439	Cf	“	“
277(9431)*§	411935	1091409	Cf	Firehole Canyon 30' X 60'	locality of Kirschbaum (1987)
278(9635)§	413545	1091510	Cf	Rock Springs 30' X 60'	Rock Springs site; UF loc. 18126, DMNH loc. 15270
279(9419)*	410959	1085455	Cf	“	3.1 m below Wasatch
280(9420)†	410959	1085455	Cf	“	“
281(9421)*	410950	1085511	Cf	“	“
282(9422)*	410950	1085510	Cf	“	“
283(9423)†	410946	1085525	Cf	“	“
284(9435)†	410940	1085529	Cf	“	“
285(9436)§	410940	1085529	Cf	“	immediately below Wasatch
286(959)§**	410945	1085527	Cf	“	immediately below Wasatch
287(9535)†#	411026	1085321	Cf	“	same level loc. 284
288(9550)#	410828	1085948	Cf	“	west slope Potter Mtn.
289(9551)†	410824	1085953	Cf	“	“
290(9555)†#	411013	1085427	Cf	“	SW of loc. 292, about same level
291(9556)*	410940	1085536	Cf	“	same level loc. 284
292(9540)§	411026	1085419	Cf	“	est. 110 m below Wasatch
293(964)*	410940	1085536	Cf	“	same level loc. 284
294(9543)†	410813	1090324	Cf	Titsworth Gap 7.5'	above Buffalo Spring
295(944)*§	412754	1084236	Cf	Sand Butte Rim NW 7.5'	bed #83 of Roehler section 12-73

USNM loc. 41- (field no.)	Latitude (N)	Longitude (W)	NALMA	USGS Quadrangle	Comment
296(945-947)*†	412738	1084153	Cf	“	?correlate to bed #104 Roehler section 12-73
297(948)*	412755	1084208	Cf	“	bed #94 of Roehler section 12-73
298(949)†	412755	1084208	Cf	“	“
299(9410)*§	412754	1084236	Cf	“	bed #83 of Roehler section 12-73
300(958)*†	412738	1084153	Cf	“	?correlate to bed #104 Roehler section 12-73
301(9512)*	412755	1084208	Cf	“	bed #94 of Roehler section 12-73
Main Body of Wasatch Fm.: Washakie Basin					
306(9434)*†	410940	1085523	Wa	Potter Mtn. 7.5'	42.7 m above base of Wasatch
307(9437)**	410940	1085529	Wa?	“	base of Wasatch
308(9438)†	410944	1085529	Wa	“	42.7 m above base of Wasatch
309(9528)§**	410940	1085529	Wa?	“	base of Wasatch
310(9539)§	410950	1085511	Wa?	“	1.3 m above base of Wasatch
311(9418)*	412023	1084618	Wa-Ly	Burley Draw 7.5'	~288 m Washakie Basin ref. section
Ramsey Ranch Member of Wasatch Fm., exclusive of Great Divide Basin					
323(9429)†#	410927	1084612	Wa-Lc	Erickson-Kent Ranch 7.5'	equal to bed #53 or #55 Roehler 1991, section D
324(9430)#	410913	1091226	Wa-Lc	Firehole Canyon 30' X 60'	see Roehler 1991 section A
325(955)†	412558	1084011	Wa-Lc	Sand Butte Rim NW 7.5'	same level as MacGinitie locality (Roehler 1979)
326(966)#	412416	1092127	Wa-Lc	Firehole Canyon 30' X 60'	
327(9424)§	405816	1084222	Wa-Lc	Canyon of Lodore 30' X 60'	see Roehler 1991 section C
328(9425)*	405835	1083935	Wa-Lc	Canyon of Lodore 30' X 60'	“
Ramsey Ranch Member of Wasatch Fm.: Great Divide Basin, Latham coal zone					
316(9541)†	414232	1075043	Wa-Ly	Rawlins 30' X 60'	Continental Divide exit
317(9542)†	414257	1074808	Wa-Ly	“	“
318(9617)†	414303	1074807	Wa-Ly	“	Latham area
319(9618)†	414313	1074810	Wa-Ly	“	“
320(9619)†	414124	1075234	Wa-Ly	“	
321(9622)†	414110	1075250	Wa-Ly	“	
322(9623)†	414152	1075006	Wa-Ly	“	Latham railway cut
Ramsey Ranch Member of Wasatch Fm.: Great Divide Basin, Sourdough and Monument coal zones					
329(9426)†	414115	1081200	Wa-Lc	Red Desert NW 7.5'	Tipton Buttes
330(9427)†	414115	1081200	Wa-Lc	“	“
331(9428)†	414115	1081200	Wa-Lc	“	“
332(957)*†	414936	1080216	Wa-Lc	Red Desert Basin 30' X 60'	N shore 12 Mile Hole
333(9510)†	414115	1081200	Wa-Lc	Red Desert NW 7.5'	Tipton Buttes, in saddle
334(9511)†	414115	1081200	Wa-Lc	“	Tipton Buttes

USNM loc. 41- (field no.)	Latitude (N)	Longitude (W)	NALMA	USGS Quadrangle	Comment
335(9513)§	415155	1080017	Wa-Lc	Red Desert Basin 30' X 60'	N shore Monument Lake
336(9514)§	415155	1080017	Wa-Lc	“	“
337(9515)*	415315	1080236	Wa-Lc	“	N of shearing pens
338(9516)*	415540	1075944	Wa-Lc	Rawlins 30' X 60'	W end Sourdough Butte
339(9517)*	415535	1075921	Wa-Lc	“	E end Sourdough Butte
340(9526)*	414936	1080216	Wa-Lc	Red Desert Basin 30' X 60'	N shore 12 Mile Hole
341(9527)†	414857	1080135	Wa-Lc	“	S shore 12 Mile Hole, USGS loc. 9179, Masursky loc. 83
342(9529)*	415535	1075921	Wa-Lc	Rawlins 30' X 60'	E end Sourdough Butte
343(9531)†	414115	1081200	Wa-Lc	Red Desert NW 7.5'	Tipton Buttes
344(9532)†	414115	1081200	Wa-Lc	“	“
345(9533)†	414115	1081200	Wa-Lc	“	“
346(9534)†	414115	1081200	Wa-Lc	“	“
347(9544)†	415546	1075954	Wa-Lc	Rawlins 30' X 60'	Sourdough Butte area
348(9545)*	415605	1080010	Wa-Lc	Red Desert Basin 30' X 60'	“
349(9546)§	415605	1080010	Wa-Lc	“	“
350(9547)*†	414937	1080133	Wa-Lc	“	N shore 12 Mile Hole
351(9548)†	415429	1075955	Wa-Lc	Rawlins 30' X 60'	Sourdough Butte area
352(9549)*†	415433	1075940	Wa-Lc	“	“
353(9552)*†	415329	1075928	Wa-Lc	“	“
354(9553)*	415204	1075738	Wa-Lc	“	N shore Monument Lake
355(9554)*†	415425	1075935	Wa-Lc	“	Sourdough Butte area
356(968)*†	415458	1081025	Wa-Lc	Red Desert Basin 30' X 60'	Siberia Ridge Road
357(969)*†	415500	1081020	Wa-Lc	“	same level loc. 356
358(9615)*	415535	1075921	Wa-Lc	Rawlins 30' X 60'	E end Sourdough Butte
359(9621)*†	415535	1075921	Wa-Lc	“	“
Luman Tongue of Green River Fm.: Washakie Basin					
367(9625)§	410808	1084912	Wa-Lc	Erickson-Kent Ranch 7.5'	
Niland Tongue of Wasatch Fm.: Great Divide and Vermilion Creek Basins					
360(9439)§	410213	1084705	Wa-Lc	Kinney Rim 30' X 60'	
361(9610)†	420159	1081259	Wa-Lc	South Pass 30' X 60'	USGS locs. 5286, 9397; loc. #4 of Pipiringos, p. 12
362(9624)†	420201	1080937	Wa-Lc	South Pass 30' X 60'	loc#5 of Pipiringos, p. A12
363(9611)§	410250	1084158	Wa-Lc	Chicken Creek SW 7.5'	
364(9612)*†	410350	1084533	Wa-Lc	Kinney Rim 30' X 60'	
Wilkins Peak Member of Green River Fm.: Green River Basin					
368(9626)§	413523	1091825	Br	Rock Springs 30' X 60'	White Mtn. Road
370(9631)§	410501	1092106	Br	Firehole Canyon 30' X 60'	Little Mtn., same level as UCMP loc. PA 116

USNM loc. 41- (field no.)	Latitude (N)	Longitude (W)	NALMA	USGS Quadrangle	Comment
427§	NW1/4 SE1/4 sec 23 T13N R106W		Br	"	Little Mtn., UF loc. 15882; same level as UCMP loc. PA 116

Notes: USNM locality numbers are prefixed with "41"; i.e., "427" = USNM locality 41427. My personal field numbers shown in parentheses. All localities are in Sweetwater County, Wyoming, except USNM localities 41327 and 41328, in Moffat County, Colorado (Fig. 5.1). Latitude-longitude data primarily from handheld GPS; from numerous cross-checks with topographic maps, I have found these readings generally to be accurate within 3". Field maps and locality photographs are available on consultation with me or from USNM collections staff. See Gemmill and Johnson (1997) for information on the Bison Basin sites. NALMA = known or inferred North American Land Mammal Age: Cf = Clarkforkian; Wa = Wasatchian; Br = Bridgerian. Ly = Lysitean; Lc = Lostcabinian.

*Carbonaceous siltstone.

[†] Carbonaceous shale.

[§] Fine-grained sandstone.

#Carbonaceous claystone, poorly laminated.

**Medium-grained sandstone.

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Figure 5.1. Geographic setting. At left, the Greater Green River Basin of southwestern Wyoming, redrawn after Roehler (1993) and Wilf et al. (in press), showing major subbasins and uplifts (gray). VC BASIN = Vermilion Creek Basin. At bottom, the study area, showing locations of fossil plant quarries (Appendix 5.1); many in close proximity appear superimposed. Names and ages of rock units as in Figure 5.2. The Bison Basin assemblage is located 25 km N from the marked symbol (Gemmill and Johnson, 1997). Groups of sites set off with lassos correspond to sections discussed in text: "Mu" = Big Multi local section; "UP" = sites along Union Pacific tracks; "SBR" = Sand Butte Rim NW section; "BD" = Brooks Draw section; "La" = sites in Latham coal zone; "SD" = sites in Sourdough-Monument coal zone. Three-digit numbers immediately adjacent to some site labels are the last three digits of the USNM locality number (Appendix 5.1). See Roehler (1992c) for a regional geologic map.

Figure 5.2. Stratigraphic framework for the eight floral assemblages (filled circles). Land Mammal age and subage boundaries after Wing et al. (1999), except Wasatchian/Bridgerian boundary after Krishtalka et al. (1987). Tfu = Fort Union Formation. Twm = Wasatch Formation: Twm = Main Body; Twrr = Ramsey Ranch Member; Twn = Niland Tongue; Twc = Cathedral Bluffs Tongue. Tg = Green River Formation: Tglu = Luman Tongue; Tgt = Tipton Shale Member; Tgw = Wilkins Peak Member; Tgl = Laney Member. Tb = Bridger Formation. Twa = Washakie Formation. Ly = Lysitean. The Paleocene/Eocene boundary is currently unresolved (Berggren et al., 1997); it is set here to the Clarkforkian/Wasatchian boundary. Early/middle Eocene boundary after Cande and Kent (1992, 1995). Solid

vertical line indicates estimated amount of stratigraphic lumping. Dashed vertical line indicates age uncertainty. See text and Figure 5.3 for further explanation and citations.

Figure 5.3. Stratigraphic framework for majority of quarries in uppermost Fort Union Formation (Tfu) and lower Wasatch Formation (Twm), not to scale. Meter levels shown to nearest whole meter. USNM plant localities shown as last three digits (Appendix 5.1). Dashed lines indicate tentative correlation. The Sand Butte Rim NW section is a portion of Roehler section 12-73 (Roehler, 1977); the mammals are discussed in Roehler (1979). The Big Multi local section is as in Wilf et al. (in press). The Brooks Draw section was measured for this paper. The portion of the Washakie Basin reference section shown, including the *Hyracotherium* FAD and the pollen data, is from Roehler (1992b).

Figure 5.4. Combined climate diagram for late Paleocene-early Eocene of Wyoming, based on leaf-margin and leaf-area analysis. Greater Green River Basin data from Table 5.1. Wind River Basin data from Wing (1991). Bighorn Basin data from Wing et al. (1999), except Tiffanian datapoint (Hickey, 1980; Wing et al., 1991).

Figure 5.5. Rarefied diversity curves for the four sampling levels with ten or more quarries. Each datapoint is the mean number of species drawn from 5000 random subsamples of all quarries at that level. (A) Mean values only for all four levels. (B) Means and error bars of ±1 standard deviation for the two most intensively sampled levels, Clarkforkian lumped and Sourdough.

Figure 5.6. Frequency vs. rank frequency data for taxa found in the four sampling levels with ten or more quarries. The vertical axis shows the proportion of quarries at a particular level at which a species was found. The horizontal axis shows ranks for each species along the frequency axis using the standard ranking algorithm; most data points represent more than one species with the same rank value. All three Paleocene levels show much higher frequency for the most frequent species than does the Sourdough assemblage, which has more heterogeneous species composition from site to site. Most frequent taxa: (Bison Basin) *Corylites* sp., "*Ampelopsis*" (*Archeampelos*) *acerifolia*, *Metasequoia occidentalis*, and aff. "*Carya*" *antiquorum* (100% each); (Big Multi) *Glyptostrobus europaeus*, 80%, *Corylites* sp., 73%, *Persites argutus*, 67%; (lumped Clarkforkian) *Corylites* sp., 63%, *P. argutus*, 57%, *G. europaeus*, 53%; (Sourdough) *Alnus* sp. (48%), *Platycarya americana* and "*Dombeya*" *novi-mundi* (45% each), *Lygodium kaulfussi* (42%), and *Zingiberopsis isonervosa* (39%).

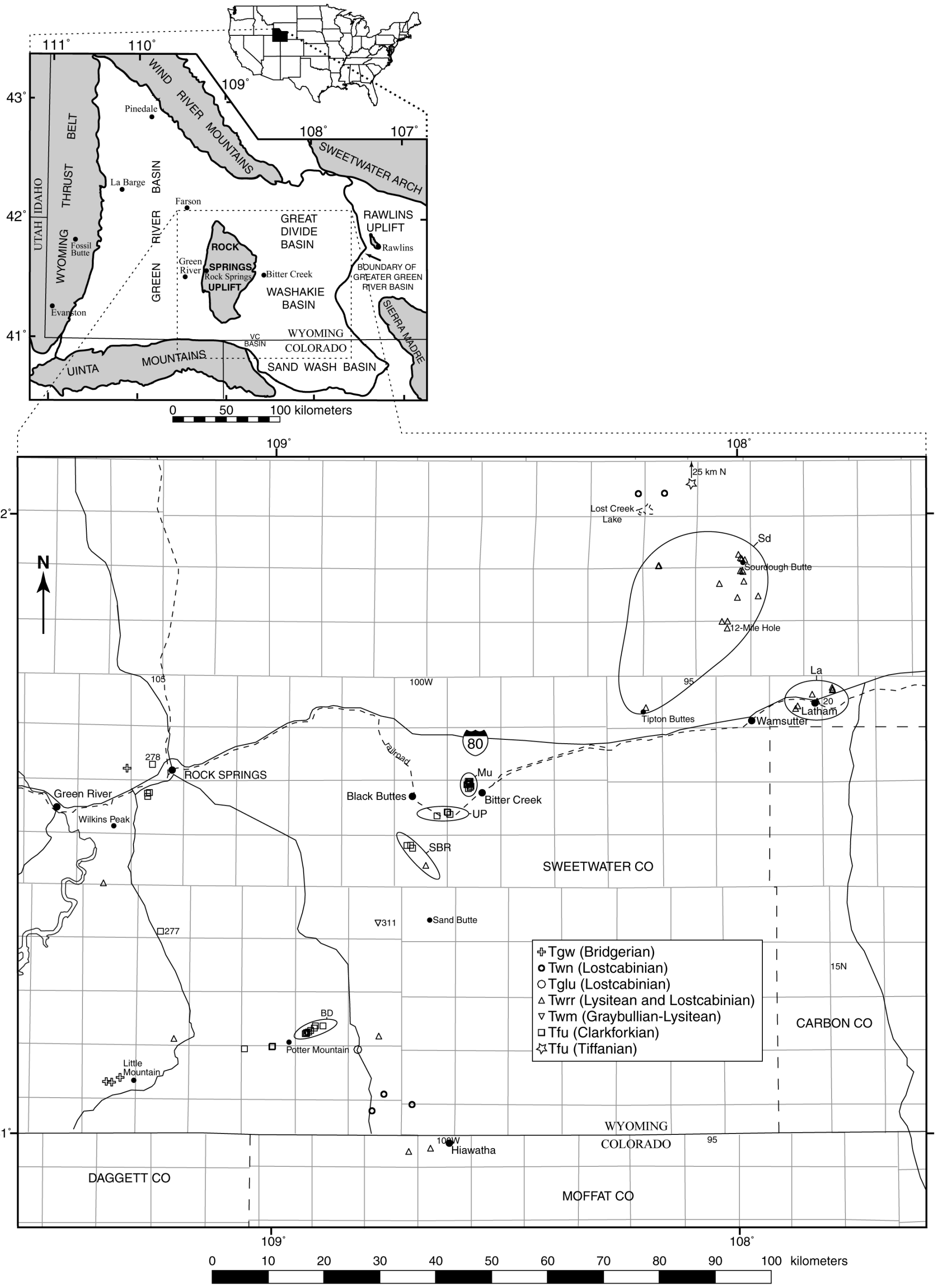

111°
110°
109°
108°
107°
43°
42°
41°
WIND RIVER MOUNTAINS
SWEETWATER ARCH
THRUST BELT
UTAH
IDAHO
WYOMING
Pinedale
La Barge
Farson
Fossil Butte
Evanston
GREEN RIVER BASIN
GREAT DIVIDE BASIN
RAWLINS UPLIFT
Rawlins
ROCK SPRINGS UPLIFT
Green River
Rock Springs
Bitter Creek
WASHAKIE BASIN
BOUNDARY OF GREATER GREEN RIVER BASIN
SIERRA MADRE
WYOMING
COLORADO
VC BASIN
UINTA MOUNTAINS
SAND WASH BASIN
0 50 100 kilometers
N
25 km N
Lost Creek Lake
Sd
Sourdough Butte
12-Mile Hole
105
100W
95
Tipton Buttes
La
Latham
20
Wamsutter
80
railroad
278
ROCK SPRINGS
Green River
Wilkins Peak
Mu
Black Buttes
Bitter Creek
UP
SBR
SWEETWATER CO
311
Sand Butte
277
15N
CARBON CO
BD
Potter Mountain
Little Mountain
WYOMING
COLORADO
95
108W
Hiawatha
DAGGETT CO
MOFFAT CO
0 10 20 30 40 50 60 70 80 90 100 kilometers
✚ Tgw (Bridgerian)
● Twn (Lostcabinian)
○ Tglu (Lostcabinian)
△ Twrr (Lysitean and Lostcabinian)
▽ Twm (Graybullian-Lysitean)
□ Tfu (Clarkforkian)
☆ Tfu (Tiffanian)

FIGURE 5.2

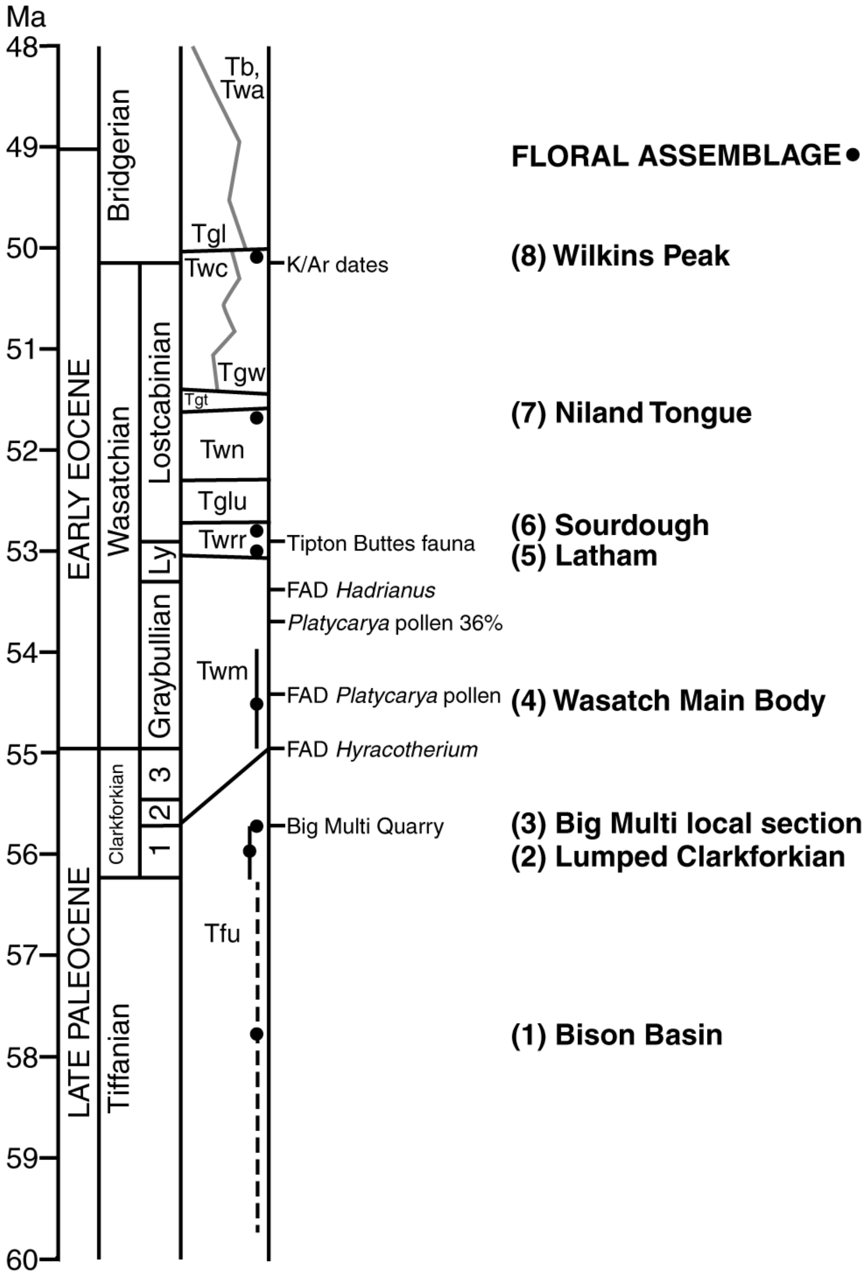
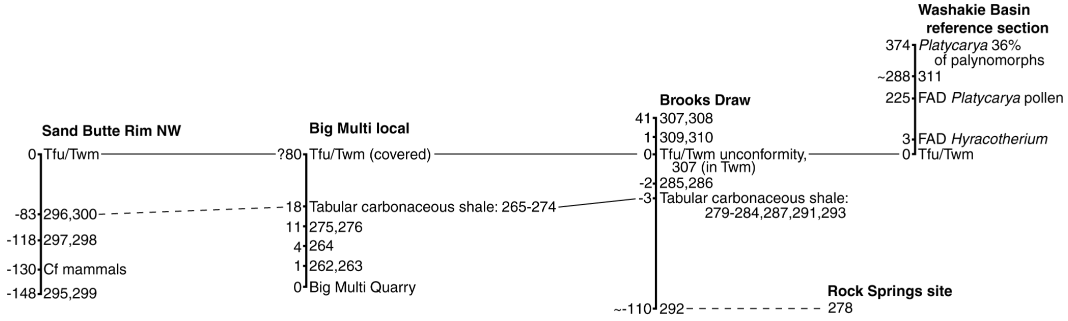
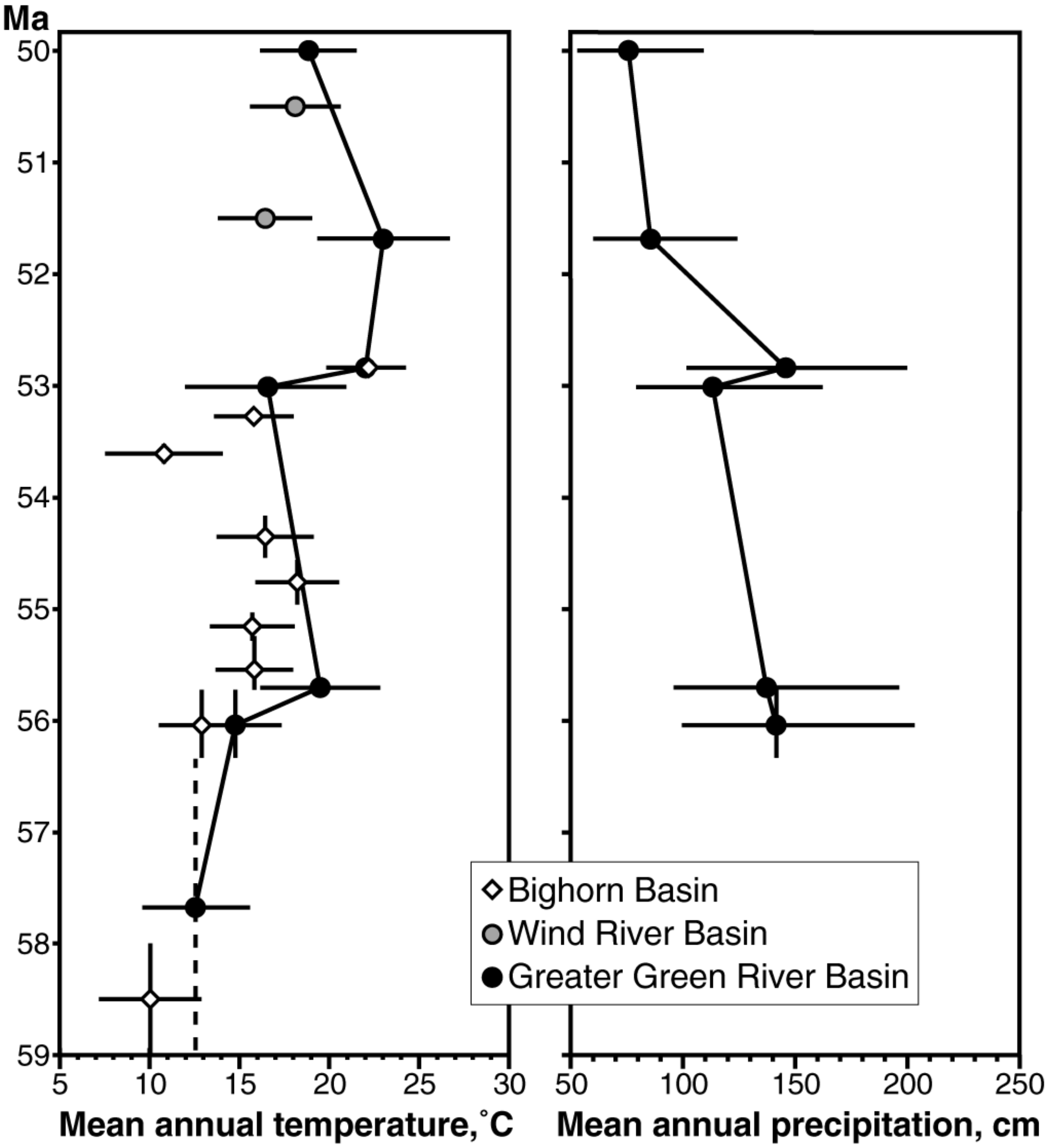
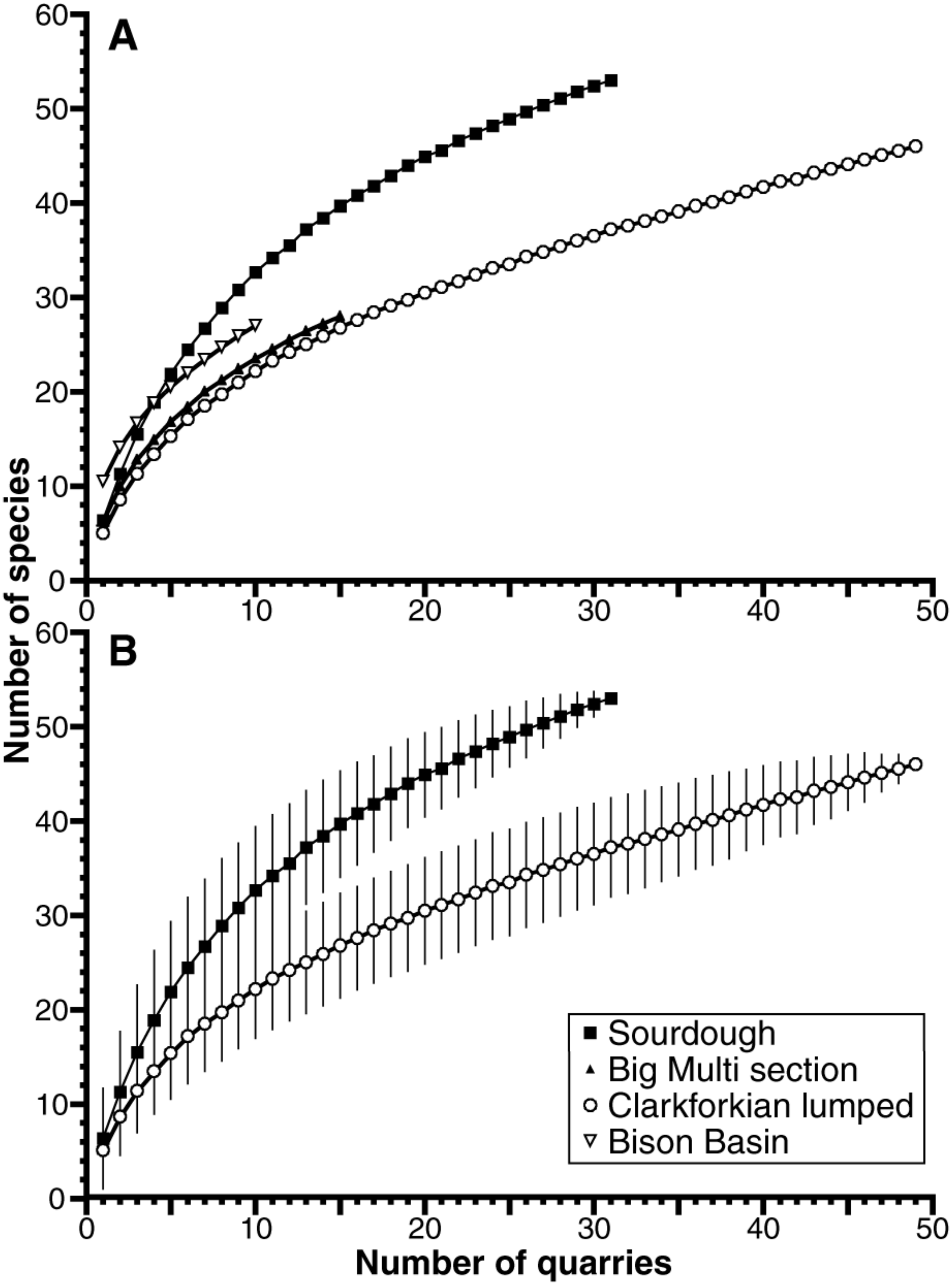
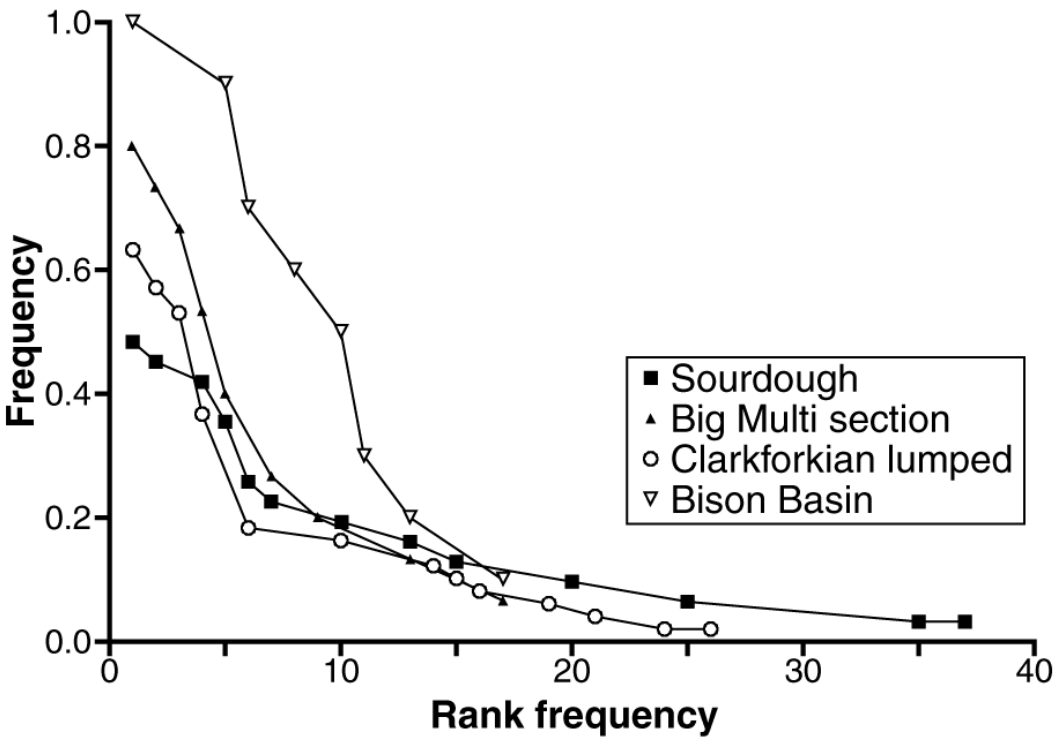

Ma
48
49
50
51
52
53
54
55
56
57
58
59
60
EARLY EOCENE
LATE PALEOCENE
Bridgerian
Wasatchian
Clarkforkian
Tiffanian
Lostcabinian
Ly
Graybullian
3
2
1
Tb, Twa
Tgl
Twc
Tgw
Tgt
Twn
Tglu
Twrr
Twm
Tfu
K/Ar dates
Tipton Buttes fauna
FAD Hadrianus
Platycarya pollen 36%
FAD Platycarya pollen
FAD Hyracotherium
Big Multi Quarry
FLORAL ASSEMBLAGE ●
(8) Wilkins Peak
(7) Niland Tongue
(6) Sourdough
(5) Latham
(4) Wasatch Main Body
(3) Big Multi local section
(2) Lumped Clarkforkian
(1) Bison Basin

FIGURE 5.3


Sand Butte Rim NW
0 Tfu/Twm
-83 296,300
-118 297,298
-130 Cf mammals
-148 295,299
Big Multi local
?80 Tfu/Twm (covered)
18 Tabular carbonaceous shale: 265-274
11 275,276
4 264
1 262,263
0 Big Multi Quarry
Brooks Draw
41 307,308
1 309,310
0 Tfu/Twm unconformity, 307 (in Twm)
-2 285,286
-3 Tabular carbonaceous shale: 279-284,287,291,293
~-110 292
Rock Springs site
278
Washakie Basin reference section
374 *Platycarya* 36% of palynomorphs
~288 311
225 FAD *Platycarya* pollen
3 FAD *Hyracotherium*
0 Tfu/Twm


Ma
50
51
52
53
54
55
56
57
58
59
5
10
15
20
25
30
Mean annual temperature,˚C
50
100
150
200
250
Mean annual precipitation, cm
◇ Bighorn Basin
● Wind River Basin
● Greater Green River Basin


A
B
Number of species
Number of quarries
0
10
20
30
40
50
60
0
10
20
30
40
50
■ Sourdough
▲ Big Multi section
○ Clarkforkian lumped
▽ Bison Basin


1.0
0.8
0.6
0.4
0.2
0.0
Frequency
0
10
20
30
40
Rank frequency
■ Sourdough
▲ Big Multi section
○ Clarkforkian lumped
▽ Bison Basin

CHAPTER SIX

THE FLORA

This chapter provides preliminary description and illustration of the late Paleocene-early Eocene fossil flora of southwestern Wyoming, presented in four sections. The first, “general descriptive data”, provides names, plate and figure citations, catalogue information, and a list of diagnostic features for each morphotype, in the order of Table 5.3. This order is predominantly alphabetical for ease of use. The second, “leaf architectural data”, is a concise table of architectural data for each dicot leaf morphotype, arranged alphabetically by morphotype number. The third is a set of 38 plates figuring the reference specimens. The plate figures are cited in and appear in the same order as the section of general descriptive data and Table 5.3. A complete occurrence matrix for the morphotypes follows the plates as an appendix.

GENERAL DESCRIPTIVE DATA

The format of this section is as follows:

> **Morphotype name (plate and figure citation): morphotype number; plant family; major plant group; organ; reference specimen number; locality where the reference specimen was found. Diagnostic features. Other morphotype numbers, if any.**

Fields with no data are omitted. If the morphotype is unnamed, the morphotype number appears in the morphotype name field. If a morphotype has more than one morphotype number because it was found in more than one section, the morphotype number of the reference specimen is shown as the morphotype number, and the additional morphotype numbers are shown in the “other morphotype numbers” field. “Diagnostic features” is not intended as a full description: see Table 6.1 for additional descriptive information. Terminology follows Hickey (1979). In some descriptions, a particularly informative specimen from the National Cleared Leaf Collection is mentioned.

Sphenopsida

EQUISETACEAE

Equisetum sp. (Pl. 1, Fig. 1): FW21; Equisetaceae; sphenopsid; axis; USNM 497978; USNM locality 41297. Axis with characteristic interlocking of basal sheaths of leaf blades at nodes. Round in cross section, vascular bundles in a ring. =WM08, RR39, GR544.

Polypodiopsida

BLECHNACEAE

Woodwardia gravida Hickey (Pl. 1, Fig. 2): FW19-47; Blechnaceae; pteridophyte; leaf/reproductive; USNM 497979; USNM locality 41295. Prominent areole parallels pinna rachis, connects pinnule midveins. Minor veins anastomosing. Teeth small, pointed, apically directed, concave/straight. Sori interconnected as single masses straddling pinnule midveins. =WM09. Sterile=FW19; fertile=FW47.

CYATHEACEAE

Cnemidaria magna Hickey (Pl. 1, Fig. 3): RR22; Cyatheaceae; pteridophyte; leaf; USNM 497980; USNM locality 41341. Rachis of 20 or more pairs of confluent, ovate pinnules. Venation is diagnostic: (from Hickey 1977) “lowest secondary on the basal side of the pinnule emerges directly from the rachis and dichotomizes approximately 1 mm above its origin; lowest secondary on the apical side of the pinnule emerges very low on the midvein, dichotomizes approximately 2 mm above its origin and runs nearly parallel to the rachis until turning sharply upward toward the sinus”. Margin entire.

DRYOPTERIDACEAE?

“Tatman fern” (Pl. 1, Fig. 4): RR21; Dryopteridaceae?; pteridophyte; leaf/reproductive; USNM 497988; USNM locality 41342. Pinna rachis with numerous pinnae (at least 11 pairs on best specimens), basally decurrent on rachis and sharp-tipped, each with up to 10-12 pairs of highly confluent, convex pinnules. Sori attached to midpoints of pinnule midveins, one sorus per pinnule.

POLYPODIACEAE?

Allantodiopsis erosa Lesquereux (Pl. 1, Fig. 5): RR32; Polypodiaceae; pteridophyte; leaf; USNM 497981; same level as USNM locality 41333. Midvein strong. Pinnule veins closely spaced at 70-80 degrees from midvein, considerably thinner than midvein, dichotomizing 1-2 times to margin. Margin erose. Serrations, prominent, apically directed (<30 degrees from midvein), closely spaced, sharp. Constant width over most of pinnule length. Pinnule bases acute/cuneate. =FW35, WM03.

“*Allantodiopsis* sp. 2” (Pl. 1, Fig. 6): RR35; Polypodiaceae; pteridophyte; leaf; USNM 497982; USNM locality 41353. Margin erose. Dichotomizing venation originates at about 80 degrees from midvein (higher than *A. erosa*, blade broader as well). One or two dichotomies per vein, first fork at midvein or within 1-3 mm from midvein.

PTERIDACEAE

Acrostichum hesperium Newberry (Pl. 1, Fig. 7): RR80; Pteridaceae; pteridophyte; leaf; USNM 497983; USNM locality 41362. Blade with leathery texture. Venation highly reticulate, forming elongate hexagonal fields oriented about 30 degrees to midvein. Margin entire.

SALVINIACEAE

Salvinia preauriculata Berry (Pl. 2, Fig. 1): RR06; Salviniaceae; pteridophyte; leaf; USNM 497984; same level as USNM locality 41321. Blade elliptic-oblong, entire. L:w about 1.5. Base rounded or cordate; apex rounded or emarginate. Midvein stout. Secondaries reticulate, long axes of fields perpendicular or acute to midvein. Tertiaries orthogonal reticulate, forming fine quadrangular mesh visible on best specimens. Margin entire.

SCHIZAEACEAE

Lygodium kaulfussi Heer (Pl. 2, Figs. 2, 3): RR07, RR07a; Schizaeaceae; pteridophyte; leaf; USNM 497985 (sterile: RR07); 497986 (fertile: RR07a); USNM locality 41332 (RR07) or USNM locality 41341(RR07a). After Manchester and Zavada (1987): sterile blade (RR07) palmate, entire, digitate-lobed (3-5 lobes). Lobes 30 to 50 degrees apart, rounded at apex. Venation high-angled, dichotomizing, tending to arc concavely downward. Fertile pinna (RR07a) consists of sporangiophores terminal to branching axis, each about 5 mm long with about 10 pairs of sori.

THELYPTERIDACEAE?

Thelypteris iddingsi (Knowlton) MacGinitie (Pl. 2, Fig. 4): RR69; Thelypteridaceae?; pteridophyte; leaf; USNM 497987; same level as USNM locality 41353. 10-12 opposite to subopposite non-dichotomizing veins per pinnule. Distal basal vein arises at or near junction of midvein and rachis; proximal basal vein arises directly from rachis, proximal to junction point with midvein. Adjacent basal veins form distinctive concave triangular areoles between pinnules, the apex in the pinnule sinus. Margin entire.

INCERTAE SEDIS

RR51 (Pl. 2, Fig. 5); pteridophyte; leaf; USNM 497989; same level as USNM locality 41362. The one specimen is the terminal 5 cm of a pinna rachis. Pinnules confluent, entire. Veins depart pinna rachis at 25-35 degrees, dichotomize up to 2 times, the first dichotomy within 1 mm of rachis. Sori marginal, on vein endings, round, about 0.6 mm diameter. Margin entire.

GR553 (Pl. 3, Fig. 1); pteridophyte; leaf; UF 15882-7376; UF locality 15882. Only one very poor specimen. Pinnules elongate; apex acute to round; confluent over < 10% of length. Midvein strong, divergence from rachis 70-80 degrees. Margin entire.

Cycadopsida

CYCADACEAE

Cycad sp. (Pl. 3, Fig. 2): FW52; Cycadaceae; cycadophyte; leaf; USNM 497991; USNM locality 41257. Rachis stout. Pinnules barely confluent, highly decurrent basally, with no midvein. Veins anastomosing.

Cycad? (Pl. 3, Fig. 3): FW26; Cycadaceae?; cycadophyte?; leaf; USNM 497992; same level as USNM locality 41281. Secondaries closely spaced, thin, parallel, non-anastomosing; serrations small, closely spaced, concave/convex to straight/convex; texture coriaceous with cuticle. =WM06.

Cycad? sp. (Pl. 3, Fig. 4): RR68; Cycadaceae?; cycadophyte; leaf; USNM 497990; USNM locality 41362. Blade pinnate, coriaceous with conspicuous tears parallel to secondaries. Midvein stout. Secondaries thin, dichotomizing once at midvein or within 1 mm of midvein, coursing parallel to each other to margin.

Pinopsida

PINACEAE

Pinus sp. (Pl. 3, Fig. 5): GR542; Pinaceae; conifer; leaf; USNM 497993; USNM locality 41427. Fascicle of 5 needles, 133 mm long, cf. *Pinus wheeleri* Cockerell, from Florissant.

Pinaceae sp. (Pl. 3, Fig. 6): GR543; Pinaceae; conifer; fruit; UCMP 153121; PA116. Winged seed, asymmetrical with rounded apex; 5 mm long, 2 mm long, incl. wing; seed elliptical, 1.5 mm by 1 mm.

TAXODIACEAE

Glyptostrobus europaeus (Brogniart) Heer (Pl. 3, Fig. 7): FW20; Taxodiaceae; conifer; leaf and cone; USNM 497994; USNM locality 41273. Taxodiaceous foliage with alternate needles, often awl-shaped. Cone box-like. Cone: USNM locality 41273. Cone scales: USNM localities 41278, 41290. Cuticle: USNM locality 41278. =RR30, GR541.

Metasequoia occidentalis Newberry, leaf (Pl. 3, Fig. 8): FW15; Taxodiaceae; conifer; reproductive; USNM 497996; USNM locality 41265.

Metasequoia occidentalis Newberry, cone (Pl. 3, Fig. 8): FW04; Taxodiaceae; conifer; leaf; USNM 497995; USNM locality 41282. Taxodiaceous conifer with opposite needles, tending to overlap along the rachis. =WM02.

Liliopsida

ARECACEAE

Sabalites/*Amesoneuron* (Pl. 4, Fig. 1): RR34; Palmae; monocot; leaf; USNM 497998; USNM locality 41362. Blade strongly plicate, the plications smoothly curved to acrodromous. Cross-veins convex, retroflexed or sinuous. Costa heavy, smooth-edged, acuminate, greatly extended into blade. Costate specimens only in Niland Tongue (*Sabalites*). Other palm leaves in the section are fragments (*Amesoneuron* Goeppert). =FW37,GR540.

CYPERACEAE?

Sedge-like fruits (Pl. 4, Fig. 2): RR53; Cyperaceae?; monocot; fruits; USNM 497999; USNM locality 41322. Achenes about 1 mm long, 0.5 mm wide with awn-like structures about 2 mm long; hundreds of specimens in close proximity on one bedding plane.

SMILACACEAE?

aff. *Smilax* (Pl. 4, Fig. 3): GR550; Smilacaceae?; monocot; leaf; UF 15882-20791; UF locality 15882. Blade ovate, base truncate, with seven acrodromous primaries. Similar to extant *S. bona-nox* L.

SPARGANIACEAE?

“*Sparganium*” *stygium* Heer (Pl. 4, Fig. 4): RR91; Sparganiaceae?; monocot; fruits; USNM 498000; 12 Mile Hole area, no formal locality. Globose cluster of sharp-tipped achenes.

ZINGIBERACEAE

Zingiberopsis isonervosa Hickey (Pl. 4, Fig. 5): RR03; Zingiberaceae; monocot; leaf; USNM 498001; USNM locality 41357. Large (macrophyll-megaphyll) monocot leaf with parallelodromous secondaries, and numerous, closely spaced, percurrent, perpendicular cross veins. = FW12, WM14.

INCERTAE SEDIS

Monocot A (Pl. 5, Fig. 1): RR86; monocot; leaf; USNM 497997; USNM locality 41364. Monocot fragments with closely spaced, parallelodromous secondaries and irregularly spaced and angled, convex, straight, or sinuous cross veins. Possibly *Peltandra primaeva* Hickey or *Musophyllum complicatum* Lesquereux, but lacking midvein or margin on which to make diagnosis.

Monocot B (Pl. 5, Fig. 2): GR513; monocot; leaf; UF 15882-20793; UF locality 15882. Fragment of monocot blade with closely spaced, parallelodromous secondaries. Cross veins straight, percurrent, not perpendicular to secondaries, spaced 0.5-1 mm apart.

Magnoliopsida

ACERACEAE

Dipteronia sp. (Pl. 5, Fig. 3): GR551; Aceraceae; dicot; fruit; UF 15882-7383’; UF locality 15882. Seed obovate, 5 mm long, 3 mm wide, surrounded by obovate membrane 13 mm long, 11 mm wide, including seed.

ANACARDIACEAE

Rhus nigricans (Lesquereux) Knowlton (Pl. 5, Fig. 4): GR529; Anacardiaceae; dicot; leaf; USNM 498004; USNM locality 41370. Blade asymmetrical, ovate to elliptic; l:w 4-8:1; base acute/asymmetrical, apex attenuate; petiolule short, slender. Intersecondaries typically run to sinuses. Secondaries consistently craspedodromous. Teeth one per secondary, regularly spaced, conspicuous, straight-edged or convex, sharp-acute or blunt.

APOCYNACEAE

Apocynaceae sp. (Pl. 5, Fig. 5): RR17; Apocynaceae; dicot; leaf; USNM 498005; USNM locality 41354. Blade ovate/elliptic, l:w >3. Midvein much thicker than secondaries. Secondaries numerous, thick, closely and regularly spaced, sharply upturned near margin. Tertiaries strongly percurrent, thick, and at about 150 degrees to midvein; tertiaries from midvein emerge perpendicular, turn downward a short distance from midvein to enter subadjacent secondary, giving a concentric appearance. Margin entire, thickened. = Apocynaceae sp. of Wing (1998).

ARALIACEAE?

aff. *Dendropanax latens* MacGinitie (Pl. 6, Fig. 1): RR60; Araliaceae; dicot; leaf; USNM 498006; USNM locality 41362. Blade consistently 3 lobed; lobe margins cuneate to concave. Midvein thick. Lateral primaries thick, opposite. Intersecondaries more obtuse than secondaries. Fimbrial vein prominent.

BETULACEAE

Alnus sp. (Pl. 6, Figs. 2,3): RR14(leaves)/RR14a(cones); Betulaceae; dicot; leaf/cone; USNM 498007(leaf), USNM 498008(cone); USNM locality 41351. Blade symmetrical/asymmetrical, ovate/elliptic. Base acute/cuneate or rounded. Areolation imperfect; freely ending veinlets multibranched, often confluent. Teeth glandular, highly variable in size, spacing, fed by secondaries, secondary branches, and auxiliary veins that run subparallel to margin in between the teeth. Cones woody, small (about 10 mm by 3 mm), consisting of spirally arranged bracts around a woody axis. = GR548. GR548 possibly a different species. Wasatch cone localities (incomplete list): USNM localities 41336, 41342, 41347, 41352, 41355, 41359.

Alnus? catkin (Pl. 6, Fig. 4): RR90; Betulaceae?; dicot; reproductive; USNM 498009; USNM locality 41342. Betuloid catkin with peduncle about 2 mm long. Possible staminate inflorescence of RR14, RR14a.

Corylites sp. (Pl. 6, Fig. 5): FW01; Betulaceae; dicot; leaf; USNM 498010; USNM locality 41291. Base cordate. Secondaries craspedodromous, occasionally forking inside margin. Agrophic veins prominent. Tertiaries strongly percurrent , generally straight. Teeth 3-4 per secondary. =WM17.

Palaeocarpinus aspinosa Manchester and Chen (Pl. 6, Fig. 6): FW16; Betulaceae; dicot; fruits; USNM 498011; USNM locality 41282. Ovate nut with acute apex and 10-15 longitudinal ribs. When found on axis, nuts are paired and pairs are arranged helically on axis. Presumed fruits of Corylites sp. (FW01): see Manchester and Chen (1996).

Betulaceae sp. catkins (Pl. 6, Fig. 7): FW67; Betulaceae; dicot; reproductive; USNM 498012; USNM locality 41296. Probable catkin of *Corylites* sp. (FW1) and *Palaeocarpinus aspinosa* (FW16).

CAPRIFOLIACEAE?

"*Viburnum*" *antiquum* (Newberry) Hollick (Pl. 7, Fig. 1): FW43; Caprifoliaceae?; dicot; leaf; USNM 498014; USNM locality 41292. Blade wide. Base cordate. Teeth large , rounded, extending to near base. Secondaries widely spaced. Tertiaries strongly opposite percurrent, moderately concentric, moderately closely spaced.

"*Viburnum*" *asperum* Newberry (Pl. 7, Fig. 2): FW39; Caprifoliaceae?; dicot; leaf; USNM 498013; USNM locality 41252. Secondaries numerous, regular, smoothly curving, often fork before margin, giving off numerous, graceful, strongly impressed, smoothly curving agrophic veins. Tertiaries strongly percurrent, closely spaced. Teeth regular, closely spaced.

CERATOPHYLLACEAE

Ceratophyllum muricatum Cham. subsp. incertum (Berry) Herendeen, Les, and Dilcher (Pl. 7, Fig. 3): GR516; Ceratophyllaceae; dicot; fruits; UF 15882-7455'; UF locality 15882. From Herendeen, Les, and Dilcher (1990): "fruits are 2.8-4.0 mm long...and 2.0 to 2.3 mm wide...and bear 8-11 lateral spines. the maximum lateral spine lengths are 1.7 to 3.3 mm".

CERCIDIPHYLLACEAE

Cercidiphyllum genetrix (Newberry) Hickey (Pl. 7, Fig. 4): FW51; Cercidiphyllaceae; dicot; leaf; USNM 498015; USNM locality 41278. Blade obovate-deltoid. Primaries actinodromous. Teeth broad, crenate, on distal edge of leaf only.

Joffrea sp. (Pl. 7, Fig. 5): FW50; Cercidiphyllaceae; dicot; fruits; USNM 498016; USNM locality 41278. Follicles 1.6-1.7 mm long, 0.8-0.9 mm wide, borne alternately on axis, elliptic, asymmetrical, with short peduncle or sessile. Longitudinal striations slightly twisted and generally unbranched, with closely spaced, fine transverse striations, as in *J. speirsii* Crane and Stockey. Associated with *Cercidiphyllum genetrix* foliage.

aff. Cercidiphyllaceae (Pl. 8, Fig. 1): FW09; Cercidiphyllaceae?; dicot; leaf; USNM 498017; USNM locality 41263. Primaries 5-actinodromous; primaries 2 and 4 suprabasally adpressed to central primary before divergence. Teeth, regular, closely spaced, crenate. Most likely Cercidiphyllaceae or Trochodendraceae.

CORNACEAE

Cornus hyperborea Heer (Pl. 8, Fig. 2): FW34; Cornaceae; dicot; leaf; USNM 498018; USNM locality 41270. Base acute; apex acuminate or elongate; l:w 2 -3 or higher. Secondaries strongly acrodromous, smoothly arching from midvein. Tertiaries thin, strongly percurrent, approximately perpendicular to midvein.

"*Viburnum*" *cupanioides* (Newberry) Brown (Pl. 8, Fig. 3): FW44; Cornaceae; dicot; leaf; USNM 498019; USNM locality 41292. Teeth on distal 2/3 of blade only, large , slightly concave to hooked apically, glandular. Secondaries widely spaced. Tertiaries strongly opposite percurrent.

ELAEOCARPACEAE?

aff. *Sloanea* (Pl. 8, Fig. 4): RR18; Elaeocarpaceae?; dicot; leaf; USNM 498020; USNM locality 41342. Prolific producer of membranaceous cuticle. L:w>2. Base acute, obtuse in basalmost portion. Basal secondaries acute. Tertiaries thick, percurrent. Margin thick, with fimbrial vein. Teeth irregularly spaced, setaceous, often cryptic. = aff. *Sloanea*, Dicot XXV of Wing (1998). Cleared leaf reference: *Sloanea hanceana* #352.

EUPHORBIACEAE

aff. *Alchornea* (Pl. 9, Fig. 1): GR546; Euphorbiaceae; dicot; leaf; UCMP 153135; PA116. Blade ovate, symmetrical; base obtuse/cuneate; apex acute; l:w 2.5. Secondaries eucamptodromous; basal pair of secondaries acute, smoothly curved. Agrophic veins well-developed, numerous (3/cm), oriented perpendicular to midvein. Tertiaries strongly opposite percurrent, oriented perpendicular to midvein. Teeth minute, closely spaced (3-4/cm), regular, glandular; venation tends to apical sinus. Cleared leaf reference: *Alchornea parviflora* #11480.

Stillingia casca Hickey (Pl. 9, Fig. 2): RR47; Euphorbiaceae; dicot; leaf; USNM 498021; USNM locality 41341. Blade symmetric, l:w>3, base acute/cuneate, about 60 degrees. Midvein thick. Secondaries thin, weak, eucamptodromous, acute pair of subsecondaries present on reference specimen. Teeth small, closely spaced, 5-10 per secondary, regular, sharp-pointed, conspicuously glandular, sometimes setaceous. Cuticle present. Latham specimen from USNM locality 41317 is not conclusive.

FAGACEAE

Fagaceae sp. (Pl. 9, Fig. 3): GR522; Fagaceae; dicot; leaf; UF 15882-7405; UF locality 15882. Blade elliptic; base slightly asymmetrical; l:w 8:1, toothed over distal 60% of blade only on the one specimen. Secondaries straight, craspedodromous; regularly spaced in toothed portion, crowded, obtuse, and thin on untoothed portion, where they enter a fimbrial vein. Intersecondaries more obtuse than secondaries. Tertiaries extremely thin, numerous.

Teeth regular, one per secondary, hooklike, concave and rounded apically, convex or straight basally; sinus rounded, apex simple.

HAMAMELIDACEAE

“*Acer*” (*Liquidambar*) *lesquereuxi* Knowlton (Pl. 9, Fig. 4): GR545; Hamamelidaceae; dicot; leaf; UCMP 153007; PA116. Blade 4-lobed (5 lobes in MacGinitie 1969), wider than long, serrate (also entire in MacGinitie 1969), entire along base; base obtuse-cordate; lobes acute with angular sinuses. Only poor secondary venation preserved in the single specimen.

HIPPOCASTANACEAE

Aesculus sp. (Pl. 9, Fig. 5): FW63; Hippocastanaceae?; dicot; leaf; DMNH 15273; DMNH locality 15270. Leaf palmately compound with 5 leaflets; terminal much longer than laterals; leaflets obovate with cuneate, untoothed bases, l:w > 3:1, petiolules short to sessile. Petiole > 55 mm long. Teeth minute.

JUGLANDACEAE

“*Carya*” *antiquorum* Newberry (Pl. 10, Fig. 1): FW30; Juglandaceae; dicot; leaf; USNM 498022; USNM locality 41289. Blade obovate, asymmetrical, l:w near 3; base acute/cuneate, entire. Secondaries eucamptodromous, closely spaced and numerous (>10 per blade). Teeth numerous, closely spaced, small (about 5 per cm). =WM01.

Palaeocarya clarnensis Manchester (Pl. 10, Fig. 2): GR531; Juglandaceae; dicot; fruits; UF 15882-7359; UF locality 15882. From Manchester (1987): "Trilobed winged fruits; lobes of wing lanceolate-obovate; central lobe 30-45 mm long, 4-10 mm wide, lateral lobes departing at 30-50 degrees form the median lobe, 20-32 mm long, 3-7 mm wide; venation of lobes dominated by the midvein and a pair of strong lateral veins just inside the margin...freely ending veinlets common...nutlet 3-5 mm wide, 3-5 mm high, usually retaining the pedicel, which is 1.5-3 mm long...”

Platycarya americana Hickey (Pl. 10, Fig. 3): RR01; Juglandaceae; dicot; leaf; USNM 498023; USNM locality 41332. Blade symmetrical or asymmetrical. L:w highly variable, from <3 to

> 6. Base with elaborated, enrolled tissue. Long petiolule. Secondaries numerous, (semi)craspedodromous, smoothly curved or upturned sharply at margin, fork just inside margin, one branch to tooth and one to superadjacent tooth. Tertiaries opposite percurrent and usually retroflexed. Areolation, tight, closed. Serrations glandular. See Manchester (1987) for revision of all fossil *Platycarya*. I use Wing and Hickey's (1984) classification here for simplicity.

Platycarya americana Hickey (Pl. 10, Fig. 4): RR70; Juglandaceae; dicot; fruits; USNM 498024; same level as USNM locality 41332. Nut about 3 mm broad, wider on distal end, with prominent attachment scar and two style tips.

Platycarya americana Hickey (Pl. 10, Fig. 5): RR02; Juglandaceae; dicot; female reproductive; USNM 498025; same level as USNM locality 41332. Spirally arranged bracts on woody rachis.

?*Platycarya americana* (Pl. 10, Fig. 6): RR75; Juglandaceae?; dicot; probable male reproductive; USNM 498026; same level as USNM locality 41336. Possible male inflorescence of *Platycarya americana*. Pollen in the inflorescence is triporate.

Platycarya castaneopsis (Lesquereux) Wing and Hickey (Pl. 11, Fig. 1): RR09; Juglandaceae; dicot; leaf; USNM 498027; USNM locality 41361. Nearly identical in all features to *P. americana* (RR01), but without elaborated basilaminar tissue.

Platycarya castaneopsis (Lesquereux) Wing and Hickey (Pl. 11, Fig. 2): RR16; Juglandaceae; dicot; fruits; USNM 498028; USNM locality 41361. Winged, bilaterally symmetrical nuts.

Pterocarya macginitii Manchester and Dilcher (Pl. 11, Fig. 3): GR532; Juglandaceae; dicot; fruits; UF 15882-7457'; UF locality 15882. From Manchester and Dilcher (1982): "Fruits consisting of a small nutlet 2-3 mm wide and 3-4 mm high, with two laterally adjoining ovoid wings. Wings 8-10 mm in maximum diameter, with entire to undulatory margins. Venation subparallel, bifurcating and rarely anastomosing along a course to the outer wing margin. Two styles diverging from the apex of the nutlet apparently oriented perpendicular to the plane of the wings. Diameter of fruit from wing tip to wing tip 17-19 mm.”

LAURACEAE

aff. *Cinnamomum* (Pl. 11, Fig. 4): RR19; Lauraceae; dicot; leaf; USNM 498030; USNM locality 41342. Blade slightly asymmetrical, l:w 2-3, base acute to cuneate/decurrent. Midvein much thicker than secondaries, preserves cuticle. Secondaries widely spaced, eucamptodromous, festooned with closely spaced brochidodromous loops; basal pair acute. Tertiaries opposite percurrent, thin, straight, widely spaced, perpendicular to primary. Intramarginal vein present. A specimen with long mine near base.

"*Cinnamomum*" *sezannense* (Pl. 11, Fig. 5): FW02; Lauraceae; dicot; leaf; USNM 498031; USNM locality 41262. Blade elliptic. Secondaries eucamptodromous with one pair acute basal secondaries diverging basally. Tertiaries strongly percurrent, closely spaced, divergence from midvein perpendicular.

"*Ficus*" *planicostata* Lesquereux (Pl. 11, Fig. 6): FW54; Lauraceae?; dicot; leaf; USNM 498037; USNM locality 41262. Basally 3-actinodromous, lateral primaries more acute than first pair of secondaries. Agrophic veins thick. Tertiaries strongly opposite straight percurrent and closely spaced, nearly perpendicular to primaries. Quaternaries opposite percurrent, oriented perpendicular to tertiaries.

aff. *Ocotea* (Pl. 12, Fig. 1): FW03; Lauraceae; dicot; leaf; USNM 498032; USNM locality 41272. Primaries pinnate to 3-actinodromous with suprabasal divergence. Basal pair of secondaries acute; apical secondaries crowded. Basal subsecondaries common. Conspicuous resin dots cover blade.

aff. *Ocotea* sp. 2 (Pl. 12, Fig. 2): GR521; Lauraceae; dicot; leaf; USNM 498033; USNM locality 41427. Blade ovate or elliptic; l:w 3-6. Basal secondaries acute, often widely separated from second pair. Agrophic veins present on broad specimens. Tertiaries and agrophic veins oriented perpendicular to midvein.

Persites argutus Hickey (Pl. 12, Fig. 3): FW08; Lauraceae; dicot; leaf; USNM 498036; USNM locality 41292. Base symmetrical or asymmetrical; apex rounded, acute, or emarginate. Tertiary divergence acute from superadjacent secondary. Areolation strongly impressed; freely ending veinlets branching, often visible with naked eye. =WM10.

Lauraceae sp. (Pl. 12, Fig. 4): FW28; Lauraceae; dicot; leaf; USNM 498035; USNM locality 41278. Blade symmetrical, ovate or elliptic; base acute; apex acuminate; l:w about 3:1. Secondaries irregularly spaced and angled. Intersecondaries common, also irregular. Marginal ultimate venation looped. Freely ending veinlets typically multibranched.

Lauraceae sp. 2 (Pl. 13, Fig. 1): RR46; Lauraceae; dicot; leaf; USNM 498034; USNM locality 41341. Blade ovate; base obtuse/rounded, sometimes asymmetrical, apex acute. Cuticle membranaceous. Secondaries widely spaced basally, crowded apically; basal secondaries thick, acute, either opposite or alternate. Subsecondaries obtuse. Agrophic veins prominent. Freely ending veinlets at 5th order. Margin thickened, outer vein loops forming fimbrial vein.

LEGUMINOSAE

Caesalpinia flumen-viridensis Herendeen and Dilcher (Pl. 13, Fig. 2): GR534; Leguminosae; dicot; fruits; UF 15882-7388; UF locality 15882. From Herendeen and Dilcher 1991: "The fossil fruits are 6.4-ca. 7.0 (estimated) cm long ... 1.8 cm wide (excluding wing), with a continuous vascularized wing along the placental suture that is 5 mm wide. The wing width is nearly constant except for tapering at the ends. The fruits are thin and membranaceous. The fruit base and apex are obtuse to blunt and rounded. The fruits bear at least seven ovules. Ovules (seeds?) are 8 mm long and 3 mm wide...The wing venation consists of a poorly organized looping pattern."

aff. *Gleditsia* (Pl. 13, Fig. 3): RR29; Leguminosae; dicot; leaf; USNM 498039; USNM locality 41362. Blade variably asymmetrical; base cuneate to acute-decurrent; l:w > 3. Secondaries thin, high-angled (about 25 deg), weakly brochidodromous. Tertiaries reticulate to form large intercostal polygons. Fourth and fifth order vein fields with long axes parallel to secondaries. Margin entire, finely crenulate.

"*Gymnocladus*" *hesperia* (Brown) MacGinitie (Pl. 13, Fig. 4): GR515; Leguminosae; dicot; leaf; UCMP 153137; PA116. Blade ovate, nearly symmetrical, l:w 3-4; apex generally falcate/attenuate, base acute/cuneate or rounded; petiolule pulvinate. Secondaries thin, numerous, regular, smoothly curved. Tertiary and higher venation not preserved. Margin thickened.

Leguminosites lesquereuxiana (Knowlton) Brown (Pl. 13, Fig. 5): GR517; Leguminosae; dicot; leaf; UCMP 153134; PA116. Blade asymmetrical; base acute/cuneate; apex acute or obtuse/rounded. Secondaries thin, numerous (8 or more), more acute on one side, consistently course directly to fimbrial vein with little or no forking. Tertiary and higher venation not preserved.

Parvileguminophyllum coloradensis (Knowlton) Call and Dilcher (Pl. 14, Fig. 1): GR520; Leguminosae; dicot; leaf; USNM 498040; USNM locality 41370; leaf twice pinnately compound (attachment not found in WY). Blade and base asymmetrical; base acute, often cuneate on one side; apex acute, often falcate; l:w high, up to 8:1. Secondaries thin, brochidodromous, regular, occasionally a basal secondary is acute on one side. Tertiaries a polygonal mesh.

Leguminosae sp. (Pl. 14, Fig. 2): GR501; Leguminosae; dicot; leaf; UF 15882-7367; UF locality 15882. Blade asymmetrical, falcate; l:w>6. Midvein weak, apically indistinct from secondaries. Secondaries thin, acrodromous, very high-angled (10-15 degrees), closely spaced, numerous.

MAGNOLIACEAE

Magnoliaceae sp. (Pl. 14, Fig. 3): FW07-22-46; Magnoliaceae; dicot; leaf; USNM 498041; USNM locality 41270. Blade elliptic; size and l:w highly variable; petiole long. Midvein stout. Tertiaries alternate percurrent to strongly opposite percurrent on large specimens. Freely ending veinlets predominantly 2-branched. A superb specimen from Roland Brown's collections in USNM at USGS locality 8911.

Magnoliaceae sp. 2 (Pl. 14, Fig. 4): RR36; Magnoliaceae; dicot; leaf; USNM 498042; USNM locality 41353. Blade asymmetrical. Midvein stout, curved. Secondaries usually adpressed to midvein. Tertiaries generally percurrent. Quinternary network orthogonal reticulate, prominent. Branching freely ending veinlets, visible with naked eye on best specimens. Margin entire with fimbrial vein.

Magnoliales sp. (Pl. 15, Fig. 1): RR12; Magnoliaceae?; dicot; leaf; USNM 498038; USNM locality 41338. Blade ovate or elliptic. Base round to acute, slightly asymmetrical. Secondaries weakly brochidodromous, weakly festooned, crowded and more obtuse at base. Outer loops form fimbrial vein. In addition to Magnoliales, some affinity to Lauraceae: see *Ocotea usamberensis*, cleared leaf #5474.

MALVACEAE-STERCULIACEAE-BOMBACACEAE

"*Dombeya*" *novi-mundi* Hickey (Pl. 15, Fig. 2): RR05; Malvaceae-Sterculiaceae-Bombacaceae; dicot; leaf; USNM 498044; USNM locality 41330. Blade usually with 3 or 5 lobes. L:w from <1 to 2. Basally actinodromous with very regular, symmetrical primaries. Agrophic veins prominent. Tertiaries strongly opposite percurrent, closely spaced, often concentric. Areolation well-developed, areoles very small (<0.2 mm), quadrangular, impressed, without freely ending veinlets. Teeth regular, glandular.

Malvales aff. *Kydia* (Pl. 16 , Fig. 1): FW61; Malvaceae-Sterculiaceae-Bombacaceae; dicot; leaf; DMNH 15279; DMNH locality 15270. Blade about as long as wide; base strongly cordate. Primaries 5 with prominent agrophic veins. Tertiaries highly concentric, very closely spaced; quaternaries alternate percurrent to random reticulate. Teeth are minute, rounded vein terminations at margin, which has a fimbrial vein. Counterpart: UF 18126-13241. Cleared leaf reference: *Kydia calycina* #10473a.

MENISPERMACEAE

aff. *Abuta* (Pl. 16, Fig. 2): GR507; Menispermaceae?; dicot; leaf; UF 15882-20788; UF locality 15882. Base round or cordate; apex rounded; petiole attachment area thick, 4x3 mm. Secondaries craspedodromous, joining prominent fimbrial vein; strongly recurved apically near margin; spacing increasing steadily basally; first pair of secondaries and first pair of agrophics emerge directly from top of petiole. Agrophic veins prominent, regular, first pair compound. Tertiaries opposite percurrent, concentric, divergence perpendicular. Cleared leaf reference: *Abuta splendida* #3929.

aff. *Atriaecarpum clarnense* Manchester (Pl. 17, Fig. 1): RR56; Menispermaceae; dicot; fruits; USNM 498045; USNM locality 41332. Bilaterally symmetrical locule cast sculptured with longitudinal rows of linear depressions, oriented subperpendicular to median groove. Reference specimen is presumably the ventral surface.

aff. *Triclisia* (Pl. 17, Fig. 2): RR72; Menispermaceae?; dicot; leaf; USNM 498047; same level as USNM locality 41332. Blade asymmetric, obovate. Secondaries eucamptodromous to brochidodromous, widely spaced. One pair acute basal subsecondaries. Quaternaries and quinternaries orthogonal reticulate, form tight vein mesh. Margin entire with fimbrial vein. Possibly with unbranched freely ending veinlets. Possible menisperm- occurs with aff. *Atriaecarpum*; similar to *Triclisia riparia*, cleared leaf reference #4516.

aff. Menispermaceae (Pl. 17, Fig. 3): RR63; Menispermaceae?; dicot; leaf; USNM 498046; USNM locality 41352. Blade reniform, l:w < 1:1. Primaries three with two subprimaries, prominent pair of basal secondaries diverges suprabasally. Primary/secondary course recurving towards center of blade. Agrophic veins prominent. Margin thickened, with fimbrial vein.

MYRTACEAE

“*Eugenia*” *americana* (Lesquereux) MacGinitie (Pl. 17, Fig. 4): RR23; Myrtaceae; dicot; leaf; USNM 498048; USNM locality 41355. Primary stout. Secondaries about 80 degrees to primary, often concave down in first 1 mm of departure, thin, very numerous (about 8/cm), subparallel, course straight to thick fimbrial vein. Intersecondaries and tertiaries faint, about 10 degrees more obtuse than secondaries (nearly perpendicular to primary). =GR514.

Paleomyrtinaea sp. Pigg, Stockey, and Maxwell (Pl. 17, Fig. 5): FW66; Myrtaceae; dicot; fruits; USNM 498049; USNM locality 41270. Globose berry, 1.5-2.5 cm diameter, filled with seeds 1-2 mm long; pericarp thick, about 1 mm.

NYMPHAEACEAE

Nymphaeaceae sp. (Pl. 18, Fig. 1): RR43; Nymphaeaceae; dicot; leaf; USNM 498051; same level as USNM locality 41332. Blade peltate-central, symmetrical, round, microphyll, with about 22 radiating primaries with one dichotomy near margin (entire). Forks of adjacent veins form loops. Outer loops form intramarginal vein. Higher venation generally random reticulate, oriented parallel to primaries.

OLACACEAE?

aff. *Schoepfia republicensis* (LaMotte) Wolfe and Wehr (Pl. 18, Fig. 2): RR44; Olacaceae?; dicot; leaf; USNM 498052; same level as USNM locality 41336. Blade ovate, symmetrical to slightly asymmetrical, base round, apex attenuate/acuminate. Secondaries <5, strongly acrodromous, none in distal portion of blade; first 2 pairs emerge from petiole, adpressed to midvein. Tertiaries thin, opposite percurrent, straight to sinuous, generally perpendicular to acute to primary.

OLEACEAE

Fraxinus sp. (Pl. 18, Fig. 3): GR535; Oleaceae; dicot; fruits; UF 15882-20575; UF locality 15882. Single-seeded elliptic fruit, 0.5 mm long and 1.5 mm wide with asymmetrical wing 5.3 mm long, only slightly wider than seed. Venation parallel. Pedicel angled, about 0.6 mm long.

PLATANACEAE

"*Ficus postartocarpoides*" (Pl. 18, Fig. 4): FW06; Platanaceae?; dicot; leaf; USNM 498056; USNM locality 41274. Teeth prominent, long, and sharp, semi-platanoid, with deep sinuses, generally triangular in aspect, extend to base (contra Leepierciea preartocarpoides), 2-3 teeth per secondary, each fed to non-glandular apex by a dichotomized secondary.

Macginitiea gracilis (Lesquereux) Wolfe and Wehr (Pl. 19, Fig. 1): FW48; Platanaceae; dicot; leaf; USNM 498054; USNM locality 41278. Blade approximately as wide as long, lobed. Lobes usually 5, with broad, rounded sinuses. Primaries palinactinodromous; agrophic veins well developed. Secondaries (veins connecting primaries) conspicuously chevroned, regular. Tertiaries percurrent, closely spaced, straight. =RR25.

Macginitiea cf. *wyomingensis* (Knowlton and Cockerell) Manchester (Pl. 19, Fig. 2): GR518; Platanaceae; dicot; leaf; UCMP 153146; PA116. Blade about as wide as long, with 5, sometimes 3 lobes; lobe sinuses deep, rounded, untoothed; petiole long. Primaries palinactinodromous. Secondaries numerous, closely spaced, craspedodromous. Agrophic veins well developed. Tertiaries thin, opposite percurrent, chevroned. Teeth usually conspicuous, strongly concave apically, sinuses prominently rounded.

Platanus sp. (Pl. 19, Fig. 3): GR552; Platanaceae; dicot; fruits; UF 15882-7362; UF locality 15882. Asymmetrical achene with stylar ring of long dispersal hairs. Occurs with *Macginitiea* cf. *wyomingensis* (GR518), lending some support to moving *M. wyomingensis* back to *Platanus*.

aff. *Platanus raynoldsi* Newberry (Pl. 19, Fig. 4): GR506; Platanaceae; dicot; leaf; UF 15882-21183; UF locality 15882. Blade ovate, asymmetrical. Primaries pinnate. Secondaries irregularly spaced, forking well inside margin. Agrophic veins prominent. Teeth conspicuous, the best developed teeth concave apically with deep, rounded sinuses; feeder veins apically deflected. Similar to “unidentified leaf”, Plate 28, Fig. 4 of MacGinitie (1969).

PROTEACEAE?

Proteaciphyllum minutum MacGinitie (Pl. 19, Fig. 5): RR84; Proteaceae?; dicot; leaf?; USNM 498057; USNM locality 41361. ?Blade (may be a tepal) elliptic to ovate, l:w ratio > 3; thick, elaborated attachment tissue. Secondaries very high-angled (10-15 degrees). Tertiaries convex to reticulate. Margin thickened. =GR527.

RHAMNACEAE

Hovenia sp. (Pl. 32, Fig. 1; identification made in proof): RR15; Rhamnaceae; dicot; leaf; USNM 498084; USNM locality 41342. Blade consistently ovate, symmetrical to asymmetrical. Petiole long. Base symmetrical or asymmetrical. Basal secondaries naked at base to first agrophic veins, acute; secondaries eucamptodromous; agrophic veins prominent, semicraspedodromous. Tertiaries thin, strongly opposite percurrent, roughly perpendicular to primaries, course straight/convex. Apparently seven vein orders. Areolation well developed, Fevs 1-branched. Teeth numerous, closely spaced, regular, with apical setae. All of these features are shared with *Hovenia* spp., such as *H. dulcis* Thunb. See also *Hovenia oregonensis* Meyer and Manchester (Meyer and Manchester, 1997).

SALICACEAE

aff. *Populus* (Pl. 20, Fig. 1): FW60; Salicaceae; dicot; leaf; UF 18126-13262; UF locality 18126. Primaries 5. Tertiaries percurrent basally to reticulate distally, generally perpendicular to primaries. Teeth salicoid, conspicuously glandular, apically directed and apically concave with setaceous apex, closely spaced. Veins enter tooth within distal half.

Populus cinnamomoides (Lesquereux) MacGinitie (Pl. 20, Fig. 2): GR528; Salicaceae; dicot; leaf; USNM 498058; USNM locality 41370. Blade ovate; l:w >4. Basal secondaries acute. Teeth conspicuously glandular, numerous, irregularly spaced and sized; apex often blunt or rounded; absent in basalmost portion of blade.

Populus wyomingiana (Berry) MacGinitie (Pl. 20, Fig. 3): RR62; Salicaceae; dicot; leaf; USNM 498059; USNM locality 41352. Blade ovate/elliptic, l:w>2, base slightly asymmetrical. Three acrodromous primaries diverge suprabasally, often with additional pair of subprimaries. Agrophic veins simple or absent. Tertiaries and long axes of quaternary meshes tend to be oriented perpendicular to midvein. Teeth glandular, variable in size, usually basally convex and apically rounded, occasionally cryptic or absent, each tooth fed by two veins from forking of main feeder vein inside margin, one branch to tooth apex, one ascending close to margin to superadjacent tooth apex.

aff. *Salix cockerelli* Brown (Pl. 20, Fig. 4): GR524; Salicaceae; dicot; leaf; USNM 498060; USNM locality 41370. L:w > 3. Midvein stout. Secondaries semicraspedodromous, angle irregular. Teeth serrate, numerous and closely spaced (to 12/cm), sinuses angular. More specimens needed for good diagnosis.

SAPINDACEAE

Allophylus flexifolia (Lesquereux) MacGinitie (Pl. 20, Fig. 5): GR547; Sapindaceae; dicot; leaf; UF 15882-7441; UF locality 15882. Blade asymmetrical; base acute, often cuneate on one side. Secondaries craspedodromous, low-angled (50-60 degrees), typically forking inside margin, entering teeth or sinuses. Intersecondaries more obtuse than secondaries. Teeth conspicuous, commonly irregularly sized and spaced, sinuses angular or rounded.

Cardiospermum coloradensis (Knowlton) MacGinitie (Pl. 21, Fig. 1): GR511; Sapindaceae; dicot; leaf; USNM 498061; USNM locality 41370. Blade asymmetrical and 2-5 lobed. Lobe size and shape irregular, sinuses rounded or angled, apices acute. Primary (secondary on pinnate leaves) divergence suprabasal. Secondaries (tertiaries on pinnate leaves) thin, angle irregular, eucamptodromous to craspedodromous. Tertiaries (quaternaries) thin, alternate percurrent to random reticulate. Margin entire, thickened, with fimbrial vein.

Koelreuteria viridifluminis (Hollick) Brown (Pl. 21, Fig. 2): GR530; Sapindaceae; dicot; fruits; UCMP 153080; PA116. Round capsule 30 mm in diameter with sharp-pointed apex and thickened attachment area at base. Midvein thick, bearing a placental wing in the lower 55%, this bearing an ovate seed 6 mm long and 5 mm wide. Venation coarsely random reticulate, weakly oriented perpendicular to midvein.

aff. Sapindaceae (Pl. 21, Fig. 3): GR525; Sapindaceae?; dicot; leaf; USNM 498062; USNM locality 41370. Blade highly asymmetrical; base acute/decurrent on one side, about 70 degrees on other; inferred pinnately compound. Petiolule slender. Secondaries more acute on narrow side, angle irregular. Teeth on wide side of blade only, irregularly sized and spaced, wide, convex.

aff. Sapindaceae sp. 2 (Pl. 21, Fig. 4): RR59; Sapindaceae?; dicot; leaf; USNM 498063; USNM locality 41342 or USNM locality 41352. Blade asymmetrical. Midvein stout, somewhat curved. Secondaries craspedodromous, course directly to sinus (character of Anacardiaceae). Intersecondaries thin when present. Tertiaries thin, percurrent. Tooth size, shape, and spacing irregular, but characteristically one tooth per secondary. Teeth fed by diminutive branch of secondary as it enters superadjacent sinus. =Dicot XXXI of Wing (1998), occurs at 621 m level of Elk Creek section in Bighorn Basin. May be same as *Allophylus flexifolia* (Lesquereux) MacGinitie.

SIMAROUBACEAE

Ailanthus lesquereuxi Cockerell (Pl. 21, Fig. 5): GR533; Simaroubaceae; dicot; fruits; UF 15882-7382; UF locality 15882. Winged fruit, length 42 mm, width 18 mm, upper margin straight to emarginate, lower convex; seed central, triangular/convex, 5 mm long and 4 mm wide, closer to upper margin. Venation parallel to reticulate. A single thick vein runs along upper margin on one side, joining seed.

THEACEAE

Ternstroemites aureavallis Hickey (Pl. 22, Fig. 1): FW29; Theaceae; dicot; leaf; USNM 498064; USNM locality 41295. Base usually acute; l:w near 3. Secondaries semicraspedodromous with closely spaced, small, glandular teeth. Tertiaries generally opposite percurrent.

aff. Theaceae (Pl. 22, Fig. 2): FW49; Theaceae?; dicot; leaf; UF 18126-13239; UF locality 18126. Secondaries first fork well inside margin and can fork up to 4 times before feeding teeth. Tertiaries alternate to opposite percurrent, markedly less regular and more opposite percurrent than *Ternstroemites aureavallis*. Teeth, small, regular, theoid, with small, pointed callous caps perched on apical portion of shallow crenulations, fed directly by ultimate forks of secondaries or by semicraspedodromous spikes from outer loops of secondaries.

aff. Theaceae sp. 2 (Pl. 22, Fig. 3): FW57; Theaceae; dicot; leaf; DMNH 15277; DMNH locality 15270. Base obtuse, sometimes acute, apex acuminate. Secondaries semicraspedodromous, numerous, apically and basally crowded. Tertiaries highly opposite percurrent and strongly impressed. Teeth small, theoid, with glandular caps. This form consistently has a wider blade and a more obtuse base than *Ternstroemites aureavallis*; the two are also from different localities.

ULMACEAE

Cedrelospermum nervosum (Newberry) Manchester (Pl. 22, Fig. 4): GR512; Ulmaceae; dicot; leaf; UCMP 153099; UCMP locality PA116; Architecture extraordinarily variable. From Manchester (1989): Attachment alternate, leaf simple (attached specimens not found in WY). Blade narrow, elliptic to ovate; l:w 2.1-9.5; apex acute/attenuate; base acute/cuneate; petiole length 1.7-6.5 mm; entire or serrate. Midvein stout. Secondaries uniform in spacing and curvature. Teeth simple, one per secondary, along whole margin or only distal portion. Freely ending veinlets present, unbranched to 2-branched.

"*Celtis*" *peracuminata* Brown (Pl. 23, Fig. 1): FW59; Ulmaceae?; dicot; leaf; DMNH 15271; DMNH locality 15270. Blade ovate; l:w about 2:1; apex long-acuminate; petiole long. Primaries 3, laterals more acute than secondaries. Secondaries semicraspedodromous, turn apically close to margin. Agrophic veins prominent. Tertiaries generally highly percurrent and moderately closely spaced. Serrations minute, closely spaced (about 10/cm), regular.

Chaetoptelea microphylla (Newberry) Hickey (Pl. 23, Fig. 2): RR50; Ulmaceae; dicot; leaf; USNM 498066; USNM locality 41341. Base cordate. Secondaries more obtuse towards base. Tertiaries thick, weakly opposite percurrent. Teeth wide, convex, with a diminutive, concave, glandular, protruding apex; compound teeth not observed.

VITACEAE?

"*Ampelopsis*" *acerifolia* Newberry (Pl. 23, Fig. 3): FW14; Vitaceae?; dicot; leaf; USNM 498067; USNM locality 41296. Blade consistently cordate, usually lobed and wider than long. Primaries usually 5. Agrophic veins prominent. Tertiaries strongly percurrent, closely spaced. Teeth wide, fed directly by major veins.

INCERTAE SEDIS

"*Astronium*" *truncatum* (Lesquereux) MacGinitie (Pl. 24, Fig. 1): GR556; Anacardiaceae?; dicot; reproductive; UF 20226; UF locality 15882. Calyx of five sepals and central seed attachment scar. Sepals elliptic/obovate, apex acute or rounded, to 14 mm long, 7 mm wide; venation nearly parallelodromous, major veins visible the length of the sepal, branching near base, with sinuous cross veins. Central scar 4 mm diameter. See MacGinitie (1953:133).

Averrhoites affinis (Newberry) Hickey (Pl. 24, Fig. 2): RR41; dicot; leaf; USNM 498053; USNM locality 41362. Leaf pinnately compound. Blade asymmetrical, petiolule stout, short. Midvein stout, much thicker than secondaries, often curved. Secondaries much stronger than tertiaries, often sharply recurved near margin. Intersecondaries and tertiaries from midvein tend to curve downward to subadjacent secondary. Tertiaries acute relative to secondaries. Fungal damage spots common and characteristic. =FW11, WM15, GR510.

Calycites sp. (5-way) (not figured): RR58; dicot; reproductive; USNM 498071: Calyx of 5 connate sepals.

Calycites sp. (6-way) (Pl. 24, Fig. 3): RR71; dicot; reproductive; USNM 498002; same level as USNM locality 41332. Calyx of six fused sepals with sharp, acute apices. =FW13. See discussion, references, and Fig. 25K in Crane et al. (1990).

"*Eucommia*" *serrata* (Newberry) Brown (Pl. 24, Fig. 4): FW45; dicot; leaf; USNM 498070; same level as USNM locality 41292. Secondaries semicraspedodromous. Blade asymmetrical. Tertiaries opposite percurrent, thin, closely spaced, about 105 degrees to midvein. Teeth size and spacing irregular.

"*Meliosma*" *longifolia* (Heer) Hickey (Pl. 24, Fig. 5): RR52; dicot; leaf; USNM 498003; USNM locality 41317. Blade ovate to elliptic with conspicuous hooked, round-sinused, irregular teeth; l:w > 3; base acute/cuneate, untoothed; apex acute to acuminate; petiole narrow. Secondaries strongly semicraspedodromous. Intersecondaries occasional, irregularly angled. Areoles small, regular quadrangles without freely ending veinlets. Some similarity to Platanaceae and Aceraceae, such as *Dipteronia*.

aff. “*Pterocarya*” *roanensis* MacGinitie (Pl. 25, Fig. 1): GR504; dicot; leaf; UF 15882-7443; UF locality 15882. Leaflet asymmetrical, ovate; l:w nearly 6; apex attenuate; base asymmetrical, acute/cuneate. Midvein thick. Secondaries numerous (>10), subopposite, weakly semicraspedodromous, course straight then upturned near margin. Intersecondaries well developed, more obtuse than secondaries. Tertiaries weakly percurrent. Teeth serrate, glandular, one per secondary.

?aquatic herb (Pl. 25, Fig. 2): FW31; dicot; leaf; USNM 498068; USNM locality 41268. Toothed probable floating aquatic with fernlike flabellate vein field, dichotomizing from base; veins terminate in sinuses, not in teeth.

aff. "*Viburnum*" *antiquum* (Pl. 25, Fig. 3): FW40; dicot; leaf; USNM 498069; USNM locality 41270. Agrophic veins prominent, diverge from 2nd pair of secondaries as well as first pair. Petiole long. Teeth wide, sharp. Tertiaries thin, strongly opposite percurrent, closely spaced. Leaf is a good match for "*Viburnum*" *antiquum sensu* Hickey (1977) but not *sensu* Brown (1962) and others, specimens of which tend to be much wider and not to have agrophics from the second pair of secondaries. The latter is kept as FW43.

RR48 (Pl. 25, Fig. 4); dicot; leaf; USNM 498096; USNM locality 41341. Blade slightly asymmetrical with asymmetrical base; apex elongate, falcate; l:w>3; many conspicuous resin dots; cuticle membranaceous. Acute, thin subsecondary consistent. Areolation imperfect with branching freely ending veinlets. =Dicot XXXVI of Wing (1998).

RR27 (Pl. 26, Fig. 1); dicot; leaf; USNM 498088; USNM locality 41348. Secondaries thin, semicraspedodromous, ascend subparallel to margin, forking into teeth. Teeth serrate, triangular, small, glandular, irregularly spaced, with long basal sinuses, straight or concave on apical side. Dicot XXXVII of Wing (1998).

FW05 (Pl. 26, Fig. 2); dicot; leaf; USNM 498072; USNM locality 41269. Basally actinodromous with three primaries; lateral primaries more acute than secondaries. Agrophic veins prominent. Teeth minute, straight/convex to concave/convex, fed by secondaries or secondary branches.

FW18 (Pl. 26, Fig. 3); dicot; leaf; USNM 498073; USNM locality 41267. Blade about as wide as long; petiole long. Primaries suprabasally 3-actinodromous with adpressed laterals and 1 pair subprimaries. Teeth minute, serrate, apically directed, glandular (mucronate), concave/convex.

FW23 (Pl. 26, Fig. 4); dicot; leaf; USNM 498074; USNM locality 41269. Tertiaries orthogonal reticulate, becoming percurrent towards apex. Midvein stout.

FW24 (Pl. 27, Fig. 1); dicot; leaf; USNM 498075; USNM locality 41274. Three prominent primaries and two smaller lateral primaries. Fourth order veins thick, random reticulate, form easily visible fields on blade. Fimbrial vein.

FW25 (Pl. 27, Fig. 2); dicot; leaf; USNM 498076; USNM locality 41296. Petiole and midvein conspicuously striated. Midvein much thicker than secondaries. Dark resin glands visible along many veins. Freely ending veinlets branching. Fimbrial vein.

FW27 (Pl. 27, Fig. 3); dicot; leaf; USNM 498077; USNM locality 41263. Blade elliptic , eucamptodromous; l:w 2-3. Tertiary divergence acute/perpendicular. Intersecondaries more obtuse than secondaries, often course downward to join subadjacent secondaries.

FW32 (Pl. 27, Fig. 4); dicot; leaf; USNM 498078; USNM locality 41279. Secondaries strongly adpressed to midvein for < 1 cm before diverging. Tertiaries prominent, alternate percurrent to random reticulate. Fimbrial vein.

FW55 (Pl. 27, Fig. 5); dicot; reproductive; USNM 498081; USNM locality 41296. Diminutive flowers < 1 cm long with at least 4, maybe 5? petals, ovary superior, pedicels of equal length, apparently from a compound inflorescence. Tepals with longitudinal veins.

FW58 (Pl. 27, Fig. 6); dicot; leaf; USNM 498080; USNM locality 41270. Rosette, apparently of leaves (10).

FW62 (Pl. 28, Fig. 1); dicot; leaf; DMNH 15282; DMNH locality 15270. Secondary angle, spacing, and branching irregular, creating brochidodromous loops of unequal size. Fimbrial vein fed by outer loops of secondaries.

FW65 (Pl. 28, Fig. 2); dicot; fruits; USNM 498055; USNM locality 41264. Compound "test-tube cleaner brush" spike of seeds or possibly anthers, > 13 cm long, about 1 cm wide, little detail visible. Associated with *Averrhoites affinis* foliage.

FW68 (Pl. 28, Fig. 3); dicot; leaf; USNM 498079; USNM locality 41274. Blade narrow, l:w>3. Base acute, slightly asymmetrical. Secondaries thin, weakly brochidodromous to eucamptodromous. Tertiaries poorly organized, random reticulate to alternate percurrent.

GR502 (Pl. 28, Fig. 4); dicot; leaf; USNM 498120; USNM locality 41427. Blade asymmetrical, pinnate; base rounded; petiole short. Secondaries thick, eucamptodromous to weakly brochidodromous, divergence 40 degrees at base; angle more acute on one side and increasing basally; one obtuse basal subsecondary present. Tertiaries opposite percurrent, closely spaced, concentric.

GR503 (Pl. 29, Fig. 1); dicot; leaf; USNM 498121; USNM locality 41370. Blade asymmetrical, ovate or elliptic. Petiole stout, long; petiolar attachment thick, semicircular, from which arise the primary, two acute basal secondaries, and two basal subsecondaries. Secondaries eucamptodromous to weakly semicraspedodromous; basal pair nearly straight, distal pairs gently curved. Agrophic veins well developed. Tertiaries generally opposite percurrent. High rank. Teeth minute to cryptic, wide or narrow/triangular, slightly glandular.

GR505 (Pl. 29, Fig. 2); dicot; leaf; UF 15882-26201; UF locality 15882. Blade symmetrical, elliptic; margin entire, straight for much of blade length; base rounded, symmetrical or asymmetrical; petiole and midvein stout. Secondaries thick, eucamptodromous, extremely regular, spacing near 10 mm, crowded and more obtuse basally, angle 35-50 degrees, course straight, gently curved in exmedial third. Tertiaries very regular, closely spaced, opposite percurrent, divergence from midvein perpendicular and immediately concentric.

GR508 (Pl. 30, Fig. 1); dicot; leaf; UF 15882-7430; UF locality 15882. Blade ovate or elliptic, unlobed or possibly lobed in one specimen. Base rounded to acute. Secondaries thick, becoming more acute basally. Intersecondaries strong when present. Agrophic veins prominent, regular. Tertiaries thick, closely spaced, percurrent, departure from midvein perpendicular.

GR509 (Pl. 30, Fig. 2); dicot; leaf; UF 15882-7408'; UF locality 15882. Blade elliptic, symmetrical, l:w near 3. Secondaries eucamptodromous, straight to gently curved, spacing even and moderate (about 10 mm), angle moderate, regular (about 35 degrees). Tertiaries thin, opposite percurrent, regularly spaced.

GR523 (Pl. 30, Fig. 3); dicot; fruits; UF 15882-7481; UF locality 15882. Indeterminate fruit with at least three hemispheric wings and acute apex.

GR526 (Pl. 30, Fig. 4); dicot; leaf; USNM 498122; USNM locality 41370. Blade 3-lobed, wider than long, base cuneate; petiole long and thin; area of blade proximal to lobes triangular. Lobes narrow, elongate, incised over 80%; sinus smoothly rounded; apex narrow-acute. Primaries diverge basally (unlike Cardiospermum); lateral primaries run close to margin before entering lobes. Secondaries thin, reticulodromous. Margin thickened, possibly revolute.

GR536 (Pl. 30, Fig. 5); dicot; fruits; USNM 498124; USNM locality 41370. Seed capsule, ovate, 8 mm long, 5 mm wide, with longitudinal dehiscence over 6 mm.

GR538 (Pl. 30, Fig. 6); dicot; reproductive; USNM 498125; USNM locality 41370. Probable bract. Blade pinnate, obovate, asymmetrical; base acute, decurrent; apex rounded; margin entire. Midvein stout. Secondaries numerous (5/cm), basally crowded, high-angled (15-20 degrees), dichotomous and elaborately anastomosing to margin.

GR539 (Pl. 30, Fig. 7); dicot; fruits; UCMP 153003; PA116. Ovate fruit 3 mm long by 2.5 wide with two leaf-like epigynous wings projecting almost 20 mm. Wings with distinct midvein and thin, high-angled secondaries. S. R. Manchester reports (pers. comm. 1998) a specimen from West Branch Creek, also one on exhibit at USNM.

GR549 (Pl. 30, Fig. 8); Lauraceae?; dicot; leaf; UF 15882-7415; UF locality 15882. Blade obovate, base asymmetrical. Secondaries thin, angle irregular, basally crowded, course straight to margin or abruptly upturned at margin with accessory loops. Intersecondaries strong. Margin thickened with prominent fimbrial vein.

GR554 (Pl. 31, Fig. 1); dicot; leaf; UF 15882-7411; UF locality 15882. Blade asymmetrical, base acute/convex, apex perpendicular/obtuse, margin entire, thickened. Secondaries brochidodromous with accessory loops, widely spaced, low-angled (50-70 degrees), angle decreasing basally.

GR555 (Pl. 31, Fig. 2); dicot; leaf; USNM 498123; USNM locality 41370. Blade ovate, asymmetrical; base broad-acute, asymmetrical, subcordate; apex acute; petiole slender. Secondaries eucamptodromous, more than 5 mm apart, more acute on one side, straight, and upturned at margin. Agrophic veins thin, short. Tertiaries thin, percurrent. Margin thick, entire, with fimbrial vein.

RR04 (Pl. 31, Fig. 3); dicot; leaf; USNM 498082; USNM locality 41322. Blade asymmetrical. Midvein thick. Secondaries moderately thin, smoothly curved. Teeth inconspicuous, glandular, one per secondary.

RR10 (Pl. 31, Fig. 4); dicot; leaf; USNM 498065; USNM locality 41342. Blade wide, l:w < 1.5. Tertiaries closely spaced, opposite percurrent, concentric. Teeth inconspicuous, glandular.

RR11 (Pl. 31, Fig. 5); dicot; fruits; USNM 498127; USNM locality 41320. Fruit with 2 hemispheric lobes, about 0.8 cm radius.

RR13 (Pl. 31, Fig. 6); dicot; leaf; USNM 498083; USNM locality 41339. Base cordate. Blade rounded, wider than long, highly asymmetric with 3 curved, forking, palinactinodromous primaries; lateral on larger half of blade thicker and longer than center primary, from which agrophic veins emerge and cover much of blade surface. Subprimaries obtuse. Tertiaries strongly percurrent, closely spaced, concentric. Some cuticle on USNM 498083.

RR15 (Pl. 32, Fig. 1): See *Hovenia* sp., p. 263 (identification made in proof).

RR20 (Pl. 32, Fig. 2); dicot; leaf; USNM 498085; USNM locality 41342. Blade asymmetrical. Midvein only slightly curved. Secondaries basally crowded. Teeth numerous, regularly spaced, apically concave with rounded sinuses, giving a hooked appearance; veins often enter sinuses as well as apices.

RR24 (Pl. 32, Fig. 3); dicot; leaf; USNM 498086; USNM locality 41342. Base asymmetrical, junction of margin and petiole asymmetrical. Petiole long. Midvein and petiole stout, petiole wider than midvein. Secondaries thick, noticeably adpressed to midvein. Tertiaries much thinner than secondaries, percurrent. Fimbrial vein.

RR26 (Pl. 32, Fig. 4); dicot; leaf; USNM 498087; USNM locality 41347. Base acute/concave, slightly asymmetrical. Secondary angle irregular; basal secondaries acute. Secondary loops angular and giving off strong exmedial branches, producing anastomosed appearance. Intersecondaries present, angle inconsistent. Tertiaries sinuous, divergence generally perpendicular, proximal divergence point exmedial to distal. Margin thickened with strong fimbrial vein. Areolation imperfect, freely ending veinlets branching.

RR31 (Pl. 33, Fig. 1); dicot; leaf; USNM 498090; USNM locality 41332. Blade obovate, symmetrical, large (notophyll-mesophyll) and long, to 15 cm, l:w nearly 6:1. Petiole and midvein stout. Base narrow, acute, and decurrent. Secondaries eucamptodromous, smoothly curving, numerous, 13 pairs visible on reference specimen. Intersecondaries more obtuse than secondaries when present. Tertiaries thin, opposite percurrent, straight to retroflexed, about 105 degrees to primary. Reference specimen has numerous subparallel mining tracks, possibly of agromyzid flies.

RR37 (Pl. 33, Fig. 2); dicot; leaf; USNM 498091; USNM locality 41353. Blade ovate, large (to macrophyll size). Base round. Both secondaries and tertiaries widely spaced. Secondaries brochidodromous with apically flattened loops. One pair obtuse basal subsecondaries. Agrophic veins prominent, thicker than tertiaries. Tertiaries strongly opposite percurrent. Nepticulid-type mining on reference specimen may be host-specific. Resembles Dicot II of Wing (1998).

RR38 (Pl. 33, Fig. 3); dicot; leaf; USNM 498092; USNM locality 41353. Base asymmetrical, l:w>2. Secondaries slightly to markedly adpressed to midvein, weakly brochidodromous, irregularly spaced. Tertiaries thin, opposite percurrent, many originate from primary.

RR40 (Pl. 33, Fig. 4); dicot; leaf; USNM 498093; USNM locality 41336. Blade markedly asymmetrical and rounded, about as wide as long, apex acute. Primaries 3, stout, strongly curved, with two smaller lateral subprimaries. Tertiaries mostly perpendicular to primaries. Areolation fine, impressed, well-developed, with many branching freely ending veinlets.

RR42 (Pl. 34, Fig. 1); dicot; leaf; USNM 498094; USNM locality 41332. Low rank leaf, weakly brochidodromous with two layers of festoons; festoons stronger than inner loops. Secondary angle irregular. Areolation imperfect, forming large, irregular fields, freely ending veinlets one or more branched.

RR45 (Pl. 34, Fig. 2); dicot; leaf; USNM 498095; USNM locality 41340. Blade and base asymmetrical. Midvein stout, slightly curved. Secondaries widely spaced, becoming more obtuse and crowded basally. Tertiaries not well distinguished from quaternaries, which form prominent quadrangular meshes. Outer vein loops form fimbrial vein.

RR49 (Pl. 34, Fig. 3); dicot; leaf; USNM 498097; USNM locality 41362. Blade coriaceous, elliptic; l:w about 3:1. Secondaries thick, nearly straight, strongly eucamptodromous, angle high (15-20 degrees) and smoothly increasing towards base. Tertiaries not visible.

RR54 (Pl. 34, Fig. 4); dicot; leaf; USNM 498098; same level as USNM locality 41321. Blade asymmetrical, apparently lobed and entire. Actinodromous, primaries 5.

RR55 (Pl. 34, Fig. 5); dicot; leaf; USNM 498099; USNM locality 41362. Secondaries eucamptodromous to slightly brochidodromous, course weak near base. Tertiaries strongly percurrent, widely spaced, oriented almost 90 degrees to midvein; tertiaries from midvein convex, joining subadjacent secondary. Areolation imperfect, can be more than one set of branching freely ending veinlets per areole. Margin slightly thickened, with fimbrial vein.

RR57 (Pl. 35, Fig. 1); dicot; leaf; USNM 498100; USNM locality 41342. Blade asymmetrical, ovate, base round, l:w<2. Midvein stout, moderately curved. Secondaries stout and widely spaced, eucamptodromous. Tertiaries thin, percurrent, widely spaced. Teeth serrate, inconspicuous to cryptic, closely and regularly spaced (4-5/cm), glandular.

RR64 (Pl. 35, Fig. 2); dicot; leaf; USNM 498101; USNM locality 41352. Blade elliptic with tapered apex, l:w>3. Secondaries diverge at right angle, sharply upturned about half distance to margin, strongly brochidodromous, widely spaced but apically crowded, with small festoons. Intersecondaries thin with perpendicular or slightly obtuse divergence. Tertiaries weakly percurrent, inconsistently angled; tertiaries from midvein course downward to subadjacent secondary. Margin entire, thickened.

RR65 (Pl. 35, Fig. 3); dicot; leaf; USNM 498102; USNM locality 41352. Blade elliptic, base convex-acute, margin entire. Secondaries subopposite, slightly acrodromous, diverging about 40 degrees, widely spaced, becoming more crowded apically. Tertiaries thin, convex.

RR66 (Pl. 35, Fig. 4); dicot; leaf; USNM 498103; USNM locality 41352. Blade and base asymmetrical. Midvein and secondaries stout. Secondaries strongly brochidodromous, widely and irregularly spaced, angle increases to nearly 90 towards base, loops broad. Fimbrial vein well expressed near base.

RR67 (Pl. 36, Fig. 1); dicot; leaf; USNM 498104; USNM locality 41341. Blade 3-lobed with rounded sinuses extending more than half distance to center of blade, about as wide as long; lobe margins convex. Secondaries strongly brochidodromous, loops occur about 3/4 distance from midvein to margin. Marginal venation looped. Areolation well developed, usually with branching freely ending veinlets.

RR73 (Pl. 36, Fig. 2); dicot; leaf; USNM 498105; same level as USNM locality 41332. Blade obovate. Secondaries high-angled, especially apically, thin, adpressed to midvein, tending to run concave down, can fork less than half of the way to the margin and again still well inside the margin. Tertiaries and quaternaries alternate percurrent to random reticulate. Margin entire, thickened.

RR74 (Pl. 36, Fig. 3); dicot; leaf; USNM 498106; same level as USNM locality 41336. Blade much wider than long, deeply 5-lobed, lobes incised to > half of length of primary, sinuses broad and rounded, entire. Lobes 4 and asymmetrical on reference specimen. Primaries basally and regularly actinodromous. Higher veins not as organized as RR67. Lacks chevron secondaries, palinactinodromy or alternate percurrent tertiaries of *Macginitiea*.

RR78 (Pl. 36, Fig. 4); dicot; leaf; USNM 498108; USNM locality 41317. Blade elliptic to ovate; l:w ratio 2-3 or higher; base asymmetrical to symmetrical; petiole narrow. Secondaries eucamptodromous; basal pair faint. Tertiaries alternate to opposite. Fourth and fifth order venation orthogonal.

RR79 (Pl. 37, Fig. 1); dicot; leaf; USNM 498109; USNM locality 41317. Blade asymmetrical to strongly asymmetrical; l:w ratio >3. Midvein thick. Secondaries moderately high-angled. Tertiaries closely spaced, thin, opposite percurrent. Fourth order veins alternate percurrent, form interlocking pentagons.

RR82 (Pl. 37, Fig. 2); dicot; leaf; USNM 498111; USNM locality 41362. Blade asymmetrical. secondaries thin; basal secondaries acute and widely spaced from next pair of secondaries, which are obtuse on the thin side of the blade and acute on the wide side. Brochidodromous on wide side, more eucamptodromous on thin side. Tertiaries widely spaced and random in orientation, most intersect midvein.

RR83 (Pl. 37, Fig. 3); dicot; leaf; USNM 498112; USNM locality 41361. Blade symmetrical, elliptic to ovate, entire; basal curvature convex. Secondaries widely spaced, eucamptodromous to weakly brochidodromous, diverge about 50 degrees. Subsecondary vein distinct. Margin thickened with fimbrial vein.

RR85 (Pl. 37, Fig. 4); dicot; leaf; USNM 498113; USNM locality 41362. Blade asymmetrical, decurrent on one side. Petiole, midvein, secondaries and margin stout, petiole width 2 mm.

RR87 (Pl. 37, Fig. 5); dicot; fruits; USNM 498114; USNM locality 41342. Elliptic fruit, 15 X 6 mm, with strong longitudinal grooves.

RR89 (Pl. 37, Fig. 6); dicot; fruits; USNM 498115; USNM locality 41352. Woody fruit 7 mm broad, 3 mm high.

WM04 (Pl. 37, Fig. 7); dicot; leaf; USNM 498116; USNM locality 41307. Blade slightly asymmetrical, elliptic, l:w 3-4, base acute. Midvein strong, slightly curved. Secondaries numerous, strongly brochidodromous with up to three sets of outer loops, the outermost forming a fimbrial vein. Intersecondaries frequent.

WM05 (not figured); dicot; leaf; USNM 498117; USNM locality 41285. Fragment with three basal primaries. Tertiaries opposite percurrent, closely spaced, convex. This poorly preserved morphotype is not distinct in the context of the whole section, only within the Main Body of the Wasatch Fm. It is not included in overall species and morphotype totals.

WM16 (Pl. 38, Fig. 1); dicot; leaf; USNM 498118; USNM locality 41308. Blade ovate, entire; apex acute, base not found. Secondaries numerous, eucamptodromous, angle irregular. Tertiaries percurrent, divergence acute/right to right/right.

WM20 (not figured); dicot; leaf; USNM 498119; USNM locality 41310. One fragmentary specimen. Secondaries moderately spaced, brochidodromous loops wide, parallel to and close to margin. Tertiaries straight, opposite percurrent, tertiaries, divergence acute/perpendicular to perpendicular/perpendicular. Margin entire, thickened. This poorly preserved morphotype is not distinct in the context of the whole section, only within the Main Body of the Wasatch Fm. It is not included in overall species and morphotype totals.

WM21 (Pl. 38, Fig. 2); dicot; leaf; USNM 498029; USNM locality 41306. Blade obovate, asymmetrical. Midvein and secondaries thick. Secondary angle somewhat irregular, 40-50 degrees; course straight or curved, becoming subparallel to margin. Tertiaries thin, opposite percurrent. Teeth serrate, apically directed, inconspicuous, irregularly spaced.

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Note: see Chapter 5 for additional references on the flora.

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LEAF ARCHITECTURAL DATA

All terminology in Table 6.1, below, is used as in Hickey (1979) or is explained in the following key.

Morphotype number: as in descriptions above.

Area: end members are shown: na = nanophyll; mi = microphyll; no = notophyll; me = mesophyll; ma = macrophyll, as defined by Webb (1959).

Shape: ov = ovate; el = elliptic; ob = obovate.

Length: width ratio: Predefined discrete categories usually used, but if the range exceeded a single category, the category was “extended”. The discrete categories are: <0.75:1; 0.75-1:1; 1.0-1.2:1; 1.2-1.5:1; 1.5-2.0:1; 2-3:1; 3-6:1; 6-10:1; >10:1.

Symmetry: s = symmetrical; a = asymmetrical; ba = only the base is asymmetrical.

Base = base shape: ac = acute; co = cordate; cu = cuneate; de = decurrent; ob = obtuse; pe = peltate-central; ro = rounded; sc = subcordate; tr = truncate.

Apex = apex shape: ac = acute; am = acuminate; at = attenuate; em = emarginate; fa = falcate; ob = obtuse; ro = rounded.

Margin: first letter = lobed (l) or unlobed (u). Second letter: crenate = c; dentate = d; entire = e; s = serrate. Example: us = unlobed and serrate.

Petiole length, petiole width: in millimeters. These figures are preliminary, usually from 1-4 specimens.

1° category = major category of primary venation: ac = actinodromous; ar = acrodromous; fl = flabellate; pa = palinactinodromous; pi = pinnate.

2° category = major category of secondary venation: ar = acrodromous; br = brochidodromous; cr = craspedodromous; eu = eucamptodromous; re = reticulodromous; sc = semicraspedodromous.

Agrophics = agrophic veins: c = compound; n = none; s = simple. Agrophic veins are prominent, comb-like veins that sweep downward from the lateral primaries or from the basal pair of secondaries towards the margin. If they give off comb-like veins themselves, they are compound agrophic veins, otherwise, they are simple agrophic veins.

2° spacing = secondary vein spacing along primary: bc = basally crowded; ac = apically crowded; ir = irregular; un = uniform.

2° angle = secondary vein angle along primary: ai = abruptly increasing toward base; in = inconsistent; sd = smoothly decreasing towards base; si = smoothly increasing towards base; un = uniform; 1a = one pair acute basal secondaries; 1o = one pair obtuse basal secondaries; 1s = more acute on one side.

Intersecondaries: ab = absent; st = strong; we = weak.

3° category = tertiary category: ap = alternate percurrent; op = opposite percurrent; or = orthogonal reticulate; rr = random reticulate.

3° course = course of tertiary veins: cv = convex; in = inconsistent; si = sinuous; re = retroflexed; rt = reticulate; st = straight.

3° angle = angle of tertiary veins in relation to primary: ac = acute; ob = obtuse; ir = irregular; pe = perpendicular.

3° var. = variability in tertiary angle to primary: db = decreasing basally; de = decreasing exmedially; ib = increasing basally; ie = increasing exmedially; in = inconsistent; un = uniform.

4° category = major category of fourth order veins: ap = alternate percurrent; op = opposite percurrent; or = orthogonal reticulate; rr = random reticulate.

5° category = major category of fifth order veins: di = dichotomizing; or = orthogonal reticulate; rr = random reticulate.

Areolation: im = imperfect; ic = incomplete; wd = well-developed.

Marginal ultimate venation: fv = fimbrial vein; lo = looped; sp = spiked.

Fevs = freely ending veinlets: ab = absent; ub = unbranched; 1b = one-branched; 2b = two or more branches. Intermediate values not shown, i.e., “ub/2b” indicates fev’s are present, with zero to two or more branches.

Highest = highest order of venation observed: as indicated.

Leaf rank: as indicated.

Tooth shape: cc = concave; cv = convex; st = straight. The apical side of the tooth is denoted by the field before the slash, the basal side by the field after the slash, i.e., “cv/cv;st/cv” denotes a leaf with teeth that are either convex apically and basally or straight apically and convex basally.

Tooth sp. = tooth spacing: ir = irregular; rg = regular.

Tooth apex: gl = glandular; mu = mucronate; se = setaceous; sm = simple.

Tooth sinus: an = angular; ro = rounded.

Teeth/cm = number of teeth per centimeter: the observed range is shown. None of the morphotypes had compound teeth.

TABLE 6.1. LEAF ARCHITECTURAL DATA

Morphotype	Area	Shape	Length:width	Symmetry	Base	Apex	Margin	Petiole length	Petiole width	1° category	2° category	Agrophics	2° spacing	2° angle	Intersecondaries	3° category
FW01	mi-me	ov-el	1.0-1.2	s	co	ac/at	us	14	1	pi	cr	s	un	ai	ab	op
FW02	mi-me	el	2-3	s	ac/ro	ac/at	ue	3	1	pi	eu	s	un	1a	ab	op
FW03	mi-me	el-ov	1.5-2.0	s	ac/ro	ac	ue	5	1	pi	br	s	ac	1a	ab	op
FW05	no	ov	1.0-1.2	s	ob		us/ls?			ac	sc?	s			ab	ap/op
FW06	mi-no	ov	1.2-1.5	s	sc	ac	us			pi	cr	n	un	ai	ab	ap
FW07-22-46	mi-ma	el	1.5-2.0	s	ac/cu	ac	ue	28	1	pi	br	n	un	un	ab/we	ap/op
FW08	na-me	el-ob	2-3	s	ac/cu	ro/em	ue			pi	br	n	un	un	we	ap
FW09	mi-no	ov-el	2-3	s	ro/sc	ro	uc	3	1	ac	sc	s				op
FW14	mi-me	ov-el	0.75-1	s	co/ob	ac	ud/ld			ac	cr	s	un	si	ab	op
FW18	mi-mi	el-ob	1.0-1.2	s	ob/cu		us	15	1	ac	sc	n			ab	ap
FW23	mi	el	1.5-2.0	s	ob		ue			pi	eu	n	un	un	ab	or/ap
FW24	mi	ov	1.5-2.0	s	ro?	ac	ue			ac	eu?	n	un	sd	ab	ap
FW25	mi-me	ov	1.2-1.5	s?	ro/ob		ue	18	1	pi	eu	n	ir	in	ab	ap
FW27	no-me	el	2-3	s	ac	at?	ue	10	2	pi	eu	n	un	un	we	op
FW28	mi-me	ov-el	2-3	s	ac	am/at	ue	3	2	pi	br	n	ir	in	st/ab	ap
FW29	na-me	ov	2-3	s	ac/de	ac/at	us			pi	sc	n	ir	un	ab/we	op
FW30	mi-no	ob	2-3	a	ac/cu	ac	us	5	1	pi	eu	n	un	un	ab	ap/op
FW31	mi	el-ob	1.0-1.2	a	ob	ob	us	4	1	fl	cr	n				
FW32	no	el	1.5-2.0	s			ue			pi	eu	n	ir	sd	ab	ap
FW34	mi-me	el-ov	2-3	s	ac/de	at/am	ue			pi	ar	n	un	un	ab	op
FW39	mi	ov	1.5-2.0	s		ac/at	us			pi	cr	s	un	un	ab	op

TABLE 6.1

Morphotype	Area	Shape	Length:width	Symmetry	Base	Apex	Margin	Petiole length	Petiole width	1° category	2° category	Agrophics	2° spacing	2° angle	Intersecondaries	3° category
FW40	mi-no	el-ob	1.5-2.0	s	ro/ob	ac	us	34	1	pi	cr	s/c	bc	1o	ab	op
FW43	mi-me	ov-el	1.0-1.2	s	co	ro/ac	ud			pi	cr	s	un	si	ab	op
FW44	me	ob	1.2-1.5	s	ob	ro	us	>21	2	pi	cr	n	bc	si	ab	op
FW45	no	el	1.5-2.0	a	ac/de	ac	us	23	1	pi	sc	n	un	un	ab	op
FW48	mi-ma	el	1.0-1.2	s	ob	ac	le	16	1	pa	br	s	un	un	ab	op
FW49	no-me	el	1.5-2.0	s	ob/ro	ac	us			pi	sc	n	bc	un	ab	ap/op
FW51	mi-mi	ob	<0.75	s	ob/cu	ro/ob	uc			ac	eu	n	ir	in	ab	ap/op
FW54	me	ov	2-3	s	ob		ue			ac	br?	s	un	un		op
FW57	mi-no	el	1.0-1.2	a	ob/ac	am/at	us	8	1	pi	sc	n	bc	si	ab	op
FW59	mi-no	ov	1.5-2.0	a	ro	am/at	us	35	1	ac	sc	s	ac	un	ab	op
FW60	mi	ov	1.2-1.5	s	ob/ro	ac	us			ac	sc	n				ap
FW61	me	ov	1.0-1.2	s	co		ud			ac	cr	s				op
FW62	no	ov-el	2-3	a	ac	ac/ob	ue			pi	br	n	ir	in	st	op
FW63	mi-me	ob	3-6	s	cu/ac	ac	us	2	1	pi	cr	n	un	un		
FW68	mi	ov	3-6	ba	ac	ac	ue			pi	br	n	ir	un	ab	ap
GR501	mi	ov	6-10	a		ac/fa	ue			pi	ar	n	un	un	ab	
GR502	na	el	1.5-2.0	a	ro/ob	ac	ue	1	0	pi	eu	n	ac	si	ab	op
GR503	na-no	ov-el	1.5-2.5	a	ro/ob	ac/am	us	22	1	pi	eu	s	ac	1a	ab	ap/op
GR504	mi	ov	3-6	a	ac/cu	at	us	7	1	pi	sc	n	ac	si	st	ap
GR505	no-me	el	2-3	ba/s	ro		ue	>20	3	pi	eu	n	un	ai	ab	op
GR506	no	ov	1.5-2.0	a	ob/de?	ac	us			pi	cr	s	ir	un	ab	ap
GR507	mi-me	el-ov	1-1.5	s	ro/co	ro	ue			pi	cr	c	ac	un	ab	op
GR508	no	ov-el	1.5-2.0	s	ob/ro	ac/at	ue/le	3	1	pi	eu	s	ir	sd	st	ap/op

TABLE 6.1

Morphotype	Area	Shape	Length:width	Symmetry	Base	Apex	Margin	Petiole length	Petiole width	1° category	2° category	Agrophics	2° spacing	2° angle	Intersecondaries	3° category
GR509	mi	el	3-6	s	ac	ac	ue			pi	eu	n	bc	un	ab	op
GR511	mi	ov	3-6	a	ac/de	ac	le	2	1	pi/ac	eu/cr	s	ir	in	ab	ap
GR512	na-mi	el-ov	2-9	s/a	ac/cu	ac/at	ud/ue			pi	cr/eu	n	un	un	ab	ap/op
GR515	na-no	ov	3-6	s	cu/ro	fa/at	ue		1	pi	eu	n	ir	un	we	
GR517	mi-no	el	2.5-3.5	a	ac/cu	ac/ob	ue		0	pi	cr	n	bc	in	ab	
GR518	no-ma	ov	1-1	s	ob	ac/at	ls	>12	1	pa	cr	s	un	un	ab	op
GR520	na-mi	el-ov	3-8	a	ac	at/fa	ue	1	0	pi	br	n	un	un/1a	we	or
GR521	mi-no	ov-el	3-6	s	ac/cu	ac/at	ue	>2	1	pi	eu	s	ac	1a	ab	op
GR522	mi	el	6-10	ba	ac/cu	ac	us	10	1	pi	cr	n	bc	ai	we	op
GR524	na	ov-el	3-6	a	ac	ac	us			pi	sc	n	un	in	ab	op
GR525	na-mi	ov	2-3	a	de/ob	ac	ud	4	0	pi	sc	n	ir	in	we	ap
GR526	na	ov	0.75-1	s	ac/cu	ac/at	le	6	0	ac	re	n	ir	in		
GR528	mi	ov	3-6	s	ac	ac/at	us			pi	eu	n	ac	1a	ab	op
GR529	mi-no	ov-el	4-8	a	ac	ac/at	us	3	0	pi	cr	n	un	un	st	op
GR545	mi	ov	<0.75	a	co/ob	ac	ls	>9	1	ac	cr					
GR546	mi	ov	2-3	s	ob/cu	ac	us			pi	eu	s	ir	1a	ab	op
GR547	mi-no	el-ov	3-6	a	ac/cu	ac/at	us			pi	cr	n	bc	sd	we	ap/op
GR549	mi	ob	2-3	ba	ac/cu		ue	8	1	pi	eu	n	bc	in	st	ap
GR554	mi	el	2-3	a	ac	ob	ue			pi	br	n	bc	sd		
GR555	mi	ov	2-3	a	ac/sc	ac	ue	10	0	pi	eu	s	ir	1s	ab	ap/op
RR01	na-no	ov-el	>3	s / a	ac/cu	ac/at	us	23	1	pi	cr	n	bc	si	ab/st	op
RR04	mi	ob	1.5-2.0	a	ac	ob	us			pi	cr	n	un	si	ab	
RR05	mi-me	ov	1.2-1.5	s	ob/co	ac	ls	9	1	ac	cr	s	ac	un	ab	op
RR09	mi	ov-el	2-6	s	cu	ac	us	8	1	pi	cr	n	un	un	st	ap/op

TABLE 6.1

Morphotype	Area	Shape	Length:width	Symmetry	Base	Apex	Margin	Petiole length	Petiole width	1° category	2° category	Agrophics	2° spacing	2° angle	Intersecondaries	3° category
RR10	me	ov	1.2-1.5	s	ro?		us			pi	sc	s	ir	un	ab	op
RR12	mi-me	el-ov	2-3	ba	ro/ac	ac	ue			pi	br	n	bc	si	we	ap
RR13	no	el	0.75-1	a	co	ro	ue			pa	br	s	ir	in	ab	op
RR14	mi-me	ov-el	1.5-2.0	s/a	cu/ro	ac	us	>3	0	pi	cr	n	un	un	ab	op
RR15	mi-no	ov	1.5-3.0	s/a	ob	ac/at	us	25	2	pi	eu	s	un	1a	ab	op
RR17	mi-no	ov-el	3-6	s	ac	ac	ue			pi	eu	n	bc	un	st/ab	op
RR18	mi-me	el	2-3	ba	ac/tr		us			pi	sc	s	un	1a	ab	op
RR19	na-no	el	2-3	a	ac/cu	at/ro	ue			pi	eu	n	un	1a	ab	op
RR20	mi-no	el	2-3	a	ac/cu	ac	us			pi	sc	n	bc	un	we	ap
RR23	mi-no	el	3-6	s	ac	ac	ue			pi	cr	n	un	un	st	op
RR24	me	ov?	1.2-1.5?	ba	ob		ue	>55	4	pi	eu?	n	un		ab	ap
RR26	mi	el	2-3	ba	ac		ue	5	1	pi	br	n	ir	1a	st	ap
RR27	no	el	2-3	s			us			pi	sc	n	un	un	we	ap/op
RR29	na-mi	ov-el	3-6	a	cu/de	ac/at	ue/ue	4	1	pi	br	n	un	un	ab	rr
RR31	no-me	ob	3-6	s	ac/de	ac	ue	12	2	pi	eu		un	si	we	or
RR36	no-me	el	2-3	a	ac/de	ro	ue			pi	eu	n	un	un	we	ap/op
RR37	no-ma	ov	1.2-1.5	s	ro/sc		ue			pi	br	s	un	un	ab	op
RR38	no	el	2-3	ba	ac		ue		1	pi	br	n	ir	un	we	op
RR40	mi-me	el	0.75-1	a	ro/ob	ac	ue			ac	eu	s	ir	in	ab	ap/op
RR41	mi-me	el-ob	var.	ba	ac/cu	ac	ue	1	1	pi	eu	n	ir	un	we/st	op
RR42	me	el	1.5-2.0	s	ro		ue			pi	br	n	ir	in	ab	ap
RR43	mi	round	1-1	s	pe		ue									
RR44	mi-no	ov	2	s/a	ro/ac	at/am	ue		1	pi	ar	n	bc	si	ab	op

TABLE 6.1

Morphotype	Area	Shape	Length:width	Symmetry	Base	Apex	Margin	Petiole length	Petiole width	1° category	2° category	Agrophics	2° spacing	2° angle	Intersecondaries	3° category
RR45	mi	el	2-3	a	ac/de		ue	2	1	pi	br	n	bc	si	we	ap
RR46	no-me	ov	1.5-2.0	ba	ob/ro	ac/fa	ue			pi	eu	s	ac	1a	we	ap/op
RR47	mi	el	3-6	s	ac/cu	ac	us	7	1	pi	eu	n	un	si	we	ap/op
RR48	mi	el-ov	3-6	ba	ac/cu	at/fa	ue	>2	1	pi	eu	n	bc	un	we	or
RR49	mi	el	3-6	s	ac	ac	ue			pi	eu	n	un	si	ab	
RR50	na-mi	ov-el	2-3	a	co	ac/at	ud			pi	cr	n	un	si	we	op
RR52	mi-no	el-ov	3-6	s	ac/cu	ac/am	us	4	1	pi	sc	n	un	si	ab/we	op
RR54	mi	ov	1.0-1.2	a	ob/ro?		le?			ac	eu	n	ir		ab	ap/op
RR55	mi-no	el	1.5-2.0	s	ac		ue			pi	eu	s	bc	un	we	op
RR57	me	ov	1.5-2.0	a	ro/ob		us			pi	eu	n	un	si	we	op
RR59	no	ov	2-6	a	ob	ac	us		1	pi	cr		ac	un	we/st	ap
RR60	no	ov	1.0-1.2	s	ac/ob	ac	le	>17	1	ac	br	s	ir	un	we	ap
RR62	mi-me	ov-el	2-3	ba	ac/de	ac	us	>10	2	ac/ar	sc	s	un	un	ab	op
RR63	mi	el	<0.75	s	co	ro	ue			ac	br	s			ab	ap
RR64	mi	el	3-6	s		ac/at	ue			pi	br		ac	un	we	ap
RR65	no	el	1.5-2.0	s	ac	ac	ue			pi	eu	n	ac	sd		op
RR66	mi	el	2-3	a	ac		ue			pi	br	n	ir	si	ab	ap
RR67	no	ov	1.0-1.2	s			le			ac	br		un	un	ab	ap
RR72	no	ob	2-3	a	ac		ue			pi	eu	n	ac	sd	ab	ap
RR73	mi	ob	2-3	s	ac		ue			pi	eu	n	un	si	ab	ap
RR74	me	ov	<0.75	s	ob	ac	le			ac	br	n	ir	in	ab	ap
RR78	mi-no	el-ov	3-6	ba	ac/cu	ac	ue	9	1	pi	eu	n	un	un	we	ap/op
RR79	mi-no	el	3-6	a	ac		ue			pi	eu	n	un	un	ab	op
RR81	mi	el-ov	3-6	a		at/am	ue			pi	br		un	?si	we	op
RR82	na	el	3-6	a	ac	am	ue			pi	eu	n	ir	1a	ab	rr

TABLE 6.1

Morphotype	Area	Shape	Length:width	Symmetry	Base	Apex	Margin	Petiole length	Petiole width	1° category	2° category	Agrophics	2° spacing	2° angle	Intersecondaries	3° category
RR83	mi-no	el-ov	1.5-2.0	s	ro/ac	ac/ro	ue		1	pi	eu	n	ir	un	ab	ap
RR84	na	el-ov	3-6	s/a	ac/cu	ro	ue			pi	eu	n	bc	un	ab	rr
RR85	mi	el	2-3	a	ac/de		ue	>6	2	pi	eu	n	un	un	ab	ap
WM04	no	el	3-6	a	ac/cu?	ac	ue			pi	br	n	un	si	we	ap
WM05	mi-no	ov?			ob		ue?			ac		s				op
WM16	mi	ov	2-3	s		ac	ue			pi	eu		un	in	ab	op
WM20	me	el?	2-3?				ue			pi	br					op
WM21	mi	ob	3-6	a	ac		us			pi	eu		bc	in	ab	ap/op

TABLE 6.1

Morphotype	3° course	3° angle	3° angle var.	4° category	5°category	Areolation	Marginal ultimate	Fevs	Highest	Rank	Tooth shape	Tooth sp.	Tooth apex	Tooth sinus	Teeth/cm
FW01	st/cv	ob	de	ap	or	wd	sp	ub	6	4	cv/cv;st/cv	rg	sm	an	3-4
FW02	st/cv	pe	ie	op	or	wd	lo	ub/1b	6	4					
FW03	st/cv	pe	ie	ap	or		lo		6?	4					
FW05	st	pe	un	ap	or	wd	lo	1b	6	3	st/cv;cc/cv;cv/cv	rg	gl	an	3
FW06	st	ob	un								cc/cv;cv/cc	rg	sm	ro	3
FW07-22-46	st/cv		un	ap	or	wd	lo	ub/2b	6	4					
FW08	si	ob	ib	or	or	wd	lo	1b/2b	6	4					
FW09	cv	pe	ie				sp				cv/cv	rg	sm	ro	3
FW14	cv/re/st	ob	ie	rr/ap	rr/or	wd	sp	ub/1b	6	3	cv/cv;cc/cv;st/cv	rg	sm	an	3
FW18	si	ob	in	rr	rr		sp			3	cc/cv	rg	mu	an	4
FW23	st/rt	ob	un	or			lo		6?	3?					
FW24	st/si	ob	in	rr	rr	im	fv	1b	6	3					
FW25	st	ob	in	rr	or	wd	fv	ub/2b	6	3					
FW27	st	pe	un												
FW28	st/re	ob	de	rr	rr	wd	lo	ub/2b	6	3					
FW29	st/si	ob	un	rr			sp		6?		cc/st	rg	gl	an	4
FW30	st/si	ob									st/cv;cc/cv;cc/cc	rg	sm	an	5
FW31											cv/cv;cv/st	rg	gl	an	6
FW32	cv	ob	un	ap	rr		fv		6?	3?					
FW34	st/cv	pe	un	ap					6?	3-4					
FW39	st	ob									cv/cv;st/cv	rg	sm	an	4
FW40	st	ob	ib	op	or		sp		6?	4	cv/cv;st/cv;st/st	rg	gl	an	3-4
FW43	st/cv	ob	ib	ap							cv/cv	rg	sm	ro	1
FW44	st/cv	ob	ib	ap			sp		6?	4?	cc/cv;st/cv	rg	gl	ro	1
FW45	st	pe	ie	ap			sp		6?	3-4	st/st;st/cv	ir	gl	an	3-4

Morphotype	3° course	3° angle	3° angle var.	4° category	5°category	Areolation	Marginal ultimate	Fevs	Highest	Rank	Tooth shape	Tooth sp.	Tooth apex	Tooth sinus	Teeth/cm
FW48	st	ob	un	or		wd	fv		5	3-4					
FW49	in	ob	in	rr	rr		sp		6	2	st/st	rg	mu	ro	4
FW51	st/cv	pe	in	ap	rr				6?	3	cv/cv	ir	sm	ro	2
FW54	st	pe	un	op			lo		6?	4					
FW57	st/cv	ob	ib								st/st	rg	mu	ro	3
FW59	st/cv	ob	un	op							cv/cv;st/cv;cc/cv	rg	sm	an	10
FW60	st/cv	pe	in	ap	or	wd	sp	ub	6	4	cc/cv	rg	se	ro	4
FW61	st/cv	pe	ie	ap	or	wd	fv	ub	6	4	cc/cc	rg	sm	ro	2
FW62	si	ob	in	ap			fv								
FW63											cc/cv	rg?	sm?		4?
FW68	si	ob	in	rr						2					
GR501															
GR502	st/cv	pe	ie	or			lo								
GR503	st/cv	pe	ie	ap	or	wd	sp	ub	7	4	cv/cv;st/st	ir	gl	ro	2-3
GR504	st/si	ob	de	or			sp			4	st/st;st/cv	rg	mu	an	1-2
GR505	st/cv	ob	ie	ap			fv								
GR506	si/cv	ob	un				sp			3-4	cc/cv;cc/st	ir	gl	ro	3
GR507	st/cv	pe	ie	op	or		fv			4					
GR508	st/cv	pe	ie	ap	or	wd	lo			4					
GR509	st/cv	ob	de	ap											
GR511	st/cv	ob	in				fv	2b							
GR512	si	pe	ie	or	or	wd	sp	ub/2b	6		cv/cv;st/cv	rg	sm	ro/an	1-4
GR515							fv								
GR517							fv								
GR518	cv	pe	ib				sp				cc/cv;cc/st	rg	sm	ro	2
GR520				rr			lo								

Morphotype	3° course	3° angle	3° angle var.	4° category	5°category	Areolation	Marginal ultimate	Fevs	Highest	Rank	Tooth shape	Tooth sp.	Tooth apex	Tooth sinus	Teeth/cm
GR521	st/cv	pe	un							3-4					
GR522	st/cv	pe	in	ap			fv			3-4	cc/cv	rg	sm	ro	1
GR524	si/st	ob	ib				sp				st/cv;st/st	rg		an	12
GR525	si/cv	ob	ib	ap			sp			3-4	cv/cv;st/cv	ir	sm	an	3-6
GR526							fv								
GR528	st/si	pe	db	rr	rr		sp			3-4	cc/cc;st/st;st/cc	ir	gl	ro	2-3
GR529	st/si	ob									st/cv;st/st;cv/cv	rg	sm	an	1-3
GR545															
GR546	st/si	pe	ie				sp				cc/cv;st/cv;cv/cv	rg	gl	ro	3-4
GR547		ob									cc/st;cc/cv;st/st	ir	gl	an/ro	2-4
GR549	st	ob	un				fv								
GR554															
GR555	st/cv	ob	un	rr			fv								
RR01	re/cv	ob	un	ap	or	wd	sp	ab	5	4	cc/cv;st/cv;st/st	rg	gl	an	5
RR04											cc/st	rg	gl	ro	2
RR05	st/cv	ob	in	ap	or	wd	sp	ab	5	4	cc/cv;st/cv	rg	gl	ro	1-3
RR09	st/si	ob	de	or	or	wd	sp		5	4	st/st;st/cc;st/cv	rg	gl	ro	2-5
RR10	st	pe	ie	ap	rr	im	sp	ub/1b	6	4	cc/cv;st/cv	ir	gl	ro	1-2
RR12	st/cv	ob	in	or	or		fv			3-4					
RR13	st	pe	ie	op	or		lo		6?	4					
RR14	st/cv	ob	ib	ap	or	im	sp	2b	6	3	cv/cv;cc/st;st/cv	ir	gl	an	2-3
RR15	st/cv	pe	ie	op	or	wd	sp	1b	7	4	cv/cv;st/st;cv/cc	rg	se	an	4
RR17	st/re	ob	un	ap	rr		lo		6?	4					
RR18	st/cv	ob	ib	ap	or		fv			4	st/st;cc/cv	ir	se	ro	1-2
RR19	st	pe	un				fv								

Morphotype	3° course	3° angle	3° angle var.	4° category	5°category	Areolation	Marginal ultimate	Fevs	Highest	Rank	Tooth shape	Tooth sp.	Tooth apex	Tooth sinus	Teeth/cm
RR20	st/si	ob	de	rr						3	cc/cv	rg	sm	ro	5
RR23	si/st	pe	un				fv								
RR24	st/si	ob													
RR26	si	ob	un	rr	rr	im	fv	1b/2b	6	2					
RR27	st/cv	ob	in	or	rr		sp			3	st/cc;cc/st	ir	gl	an	3-4
RR29	rt	ob	ib	or	or	ic	lo	ub/1b	6	3					
RR31	re/st	ob	ib	ap	rr		fv			3					
RR36	st	ob	de	ap	or	wd	fv	1b/2b	6	4					
RR37	st/cv	pe	ie	ap	rr		lo		6?	4					
RR38	st/cv	ob	ib	ap	rr					3-4					
RR40	st/cv	pe	un	or	or	wd	fv	ub/2b	6	4					
RR41	si/cv	ob	un	or	rr		lo		6?	3					
RR42	cv	ob	in	rr	rr	im	lo	1b/2b	6	2					
RR43															
RR44	st/si	pe/ac	ib	rr			fv								
RR45	st	ob	in	or			fv								
RR46	cv/st	ob	ie	or	di	im	lo	1b	5	3					
RR47	st/si	ob	ib				sp				st/cv;cc/cv	rg	gl/se	an	6-7
RR48				or	rr	im	lo	1b/2b	6	2					
RR49															
RR50	st/si	ob	ib	ap			sp			3-4	cv/cv	rg	gl	an	3-5
RR52	st	ob	ib	op	or	wd	sp	ab	6	4	cc/cv;cc/cc	ir	se	ro	3-5
RR54	st/cv	pe	ie	ap	or	im	lo	ub/1b	6	3					
RR55	st/si	pe	un	rr	rr	im	fv	1b/2b	6	3					
RR57	st	ob	de	ap	rr		sp			3	cv/cv;st/cv;st/st	rg	gl	ro	4-5
RR59	si	ob	in	ap	rr		sp			2-3	cc/st;st/st;st/cc	ir	gl?	ro	1

TABLE 6.1

Morphotype	3° course	3° angle	3° angle var.	4° category	5°category	Areolation	Marginal ultimate	Fevs	Highest	Rank	Tooth shape	Tooth sp.	Tooth apex	Tooth sinus	Teeth/cm
RR60		ob	in	or	rr	wd	fv	ub/2b	6	4					
RR62	st/cv	pe	ie	ap	or		sp				cc/cv;st/cv	ir	gl	an	2-3
RR63	cv	ob		or			fv								
RR64	st/cv	ob	in	rr	rr		fv		6?	2-3					
RR65	cv	ob	ib	or											
RR66	st	ob	de	rr	rr	wd	fv	1b	6	3					
RR67	st	ob	in	or	or	wd	lo	1b/2b	6	4					
RR72	st/cv	ob	ib	or	or	wd	lo	1b?	6?	4					
RR73	in	ob	in	rr			fv			2					
RR74															
RR78	st/cv	ob	un	or	or		fv		6?	4					
RR79	st	ob	de	ap	rr	im	lo	1b	6	3					
RR81	st/cv	ob	un				fv								
RR82	in	ir	in	rr	rr		lo			1-2					
RR83	cv/si	ob	in	rr	or	wd	fv	ub/1b	6	3					
RR84	cv/rt	ob	ib	rr			fv			2					
RR85		ob					fv								
WM04	st/cv	ob	de	rr	or	wd	lo	ub/1b	6	4					
WM05	cv	ac													
WM16	st/cv	ob	un	rr			lo								
WM20	st	ob		or			lo								
WM21	st	ob	ib	rr							cc/cv;st/cv	ir	gl	ro	2

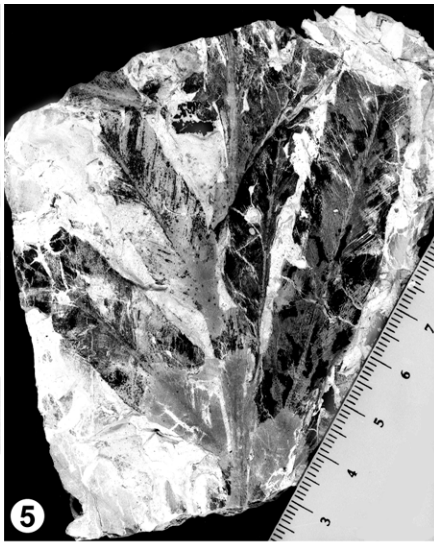
PLATES

All tick scales are in millimeters. All bar scales are in centimeters.

PLATE 1


1


2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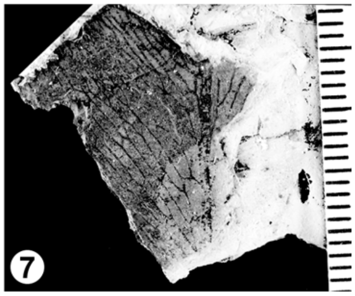
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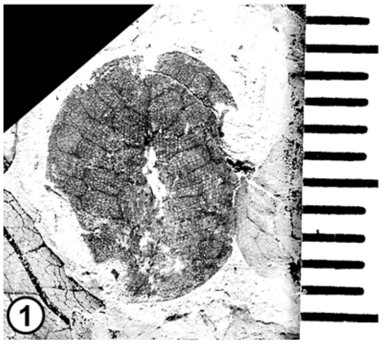
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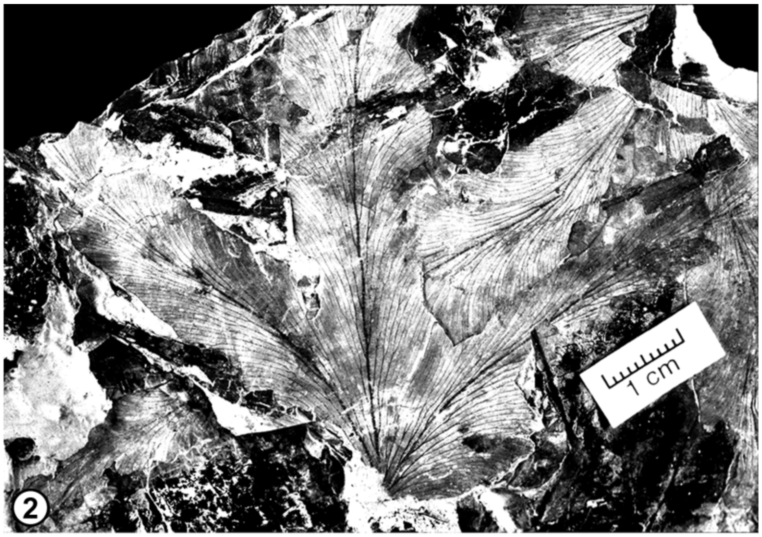
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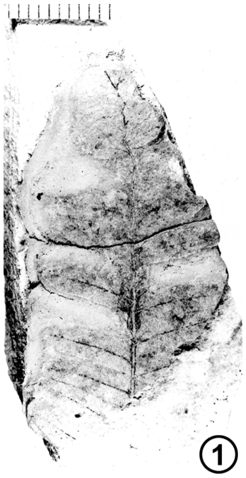
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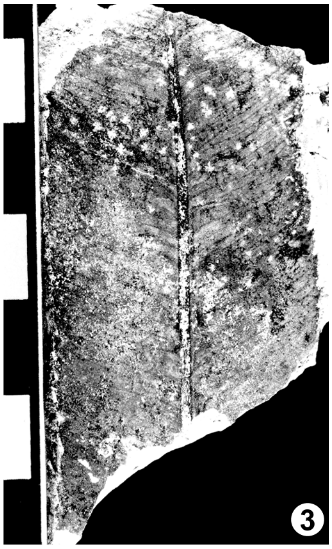
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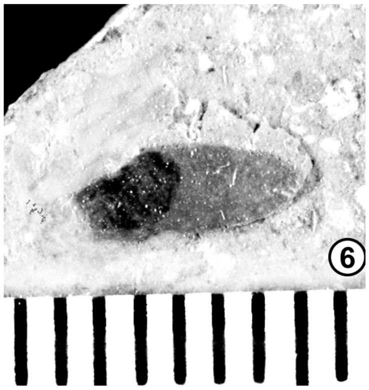
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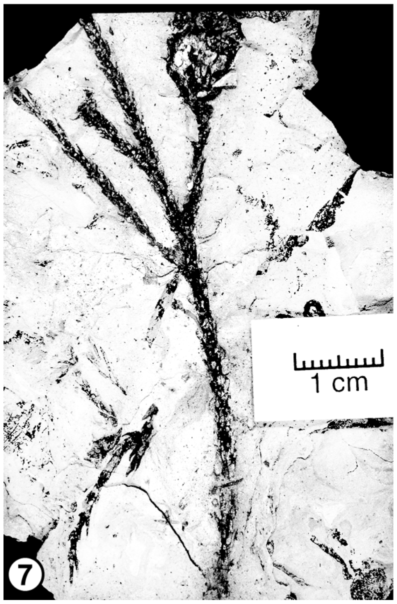

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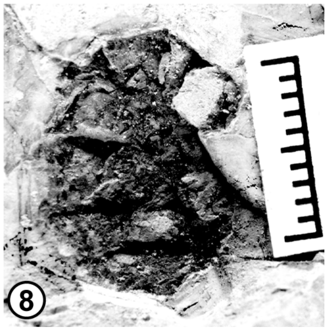
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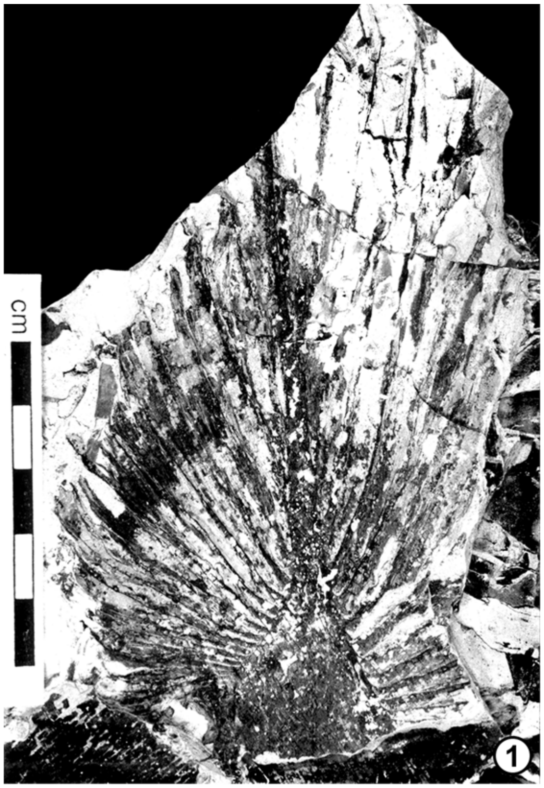

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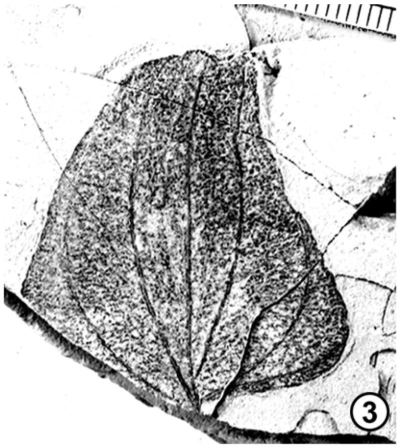

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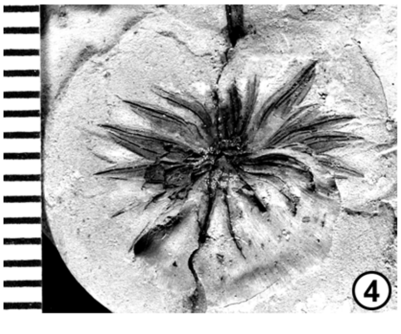

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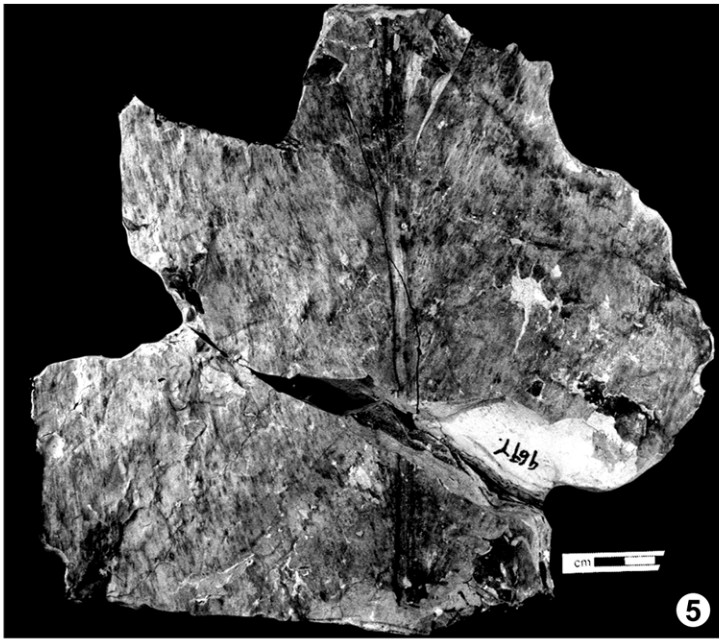

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PLATE 5


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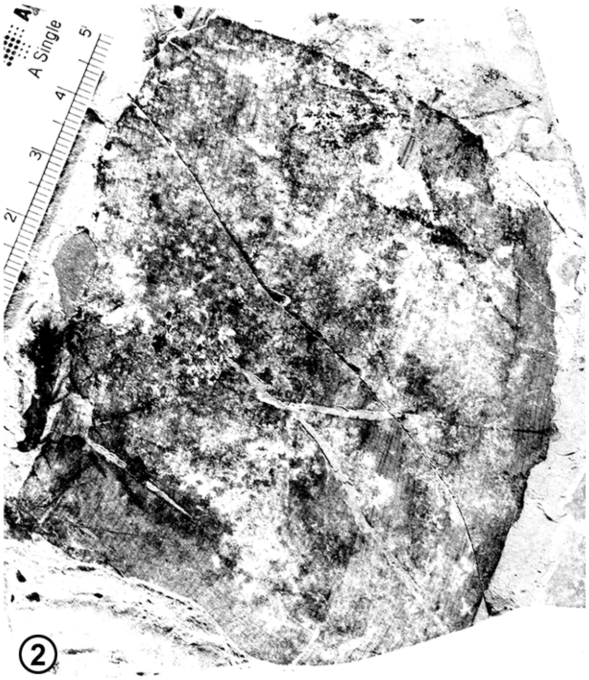

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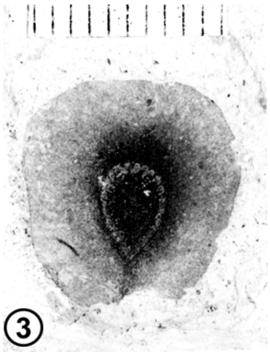
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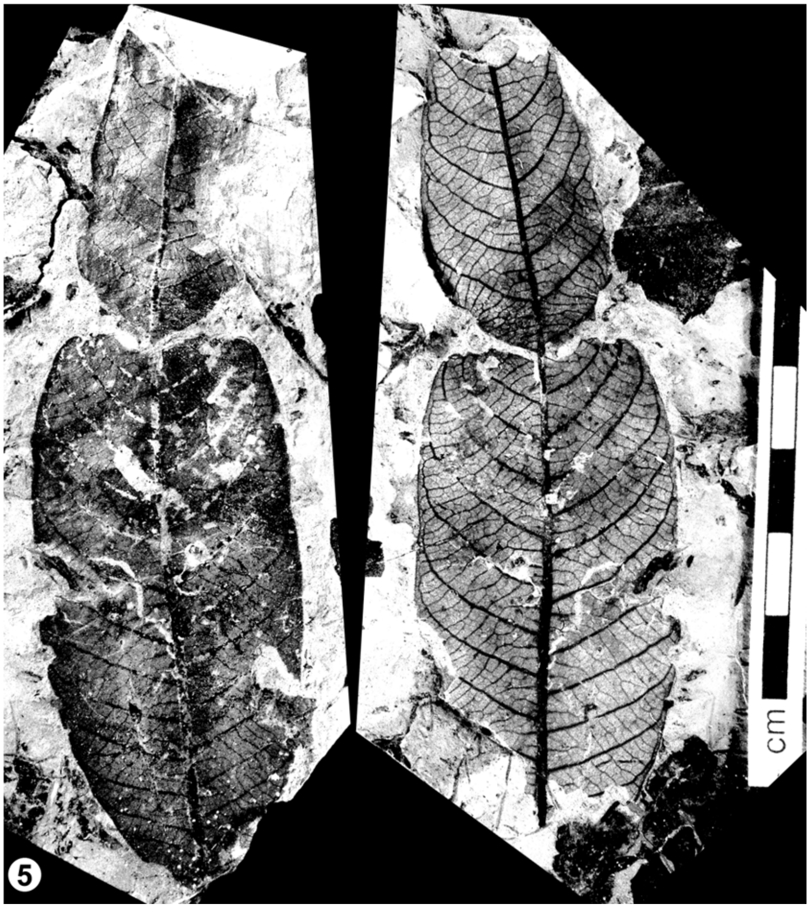

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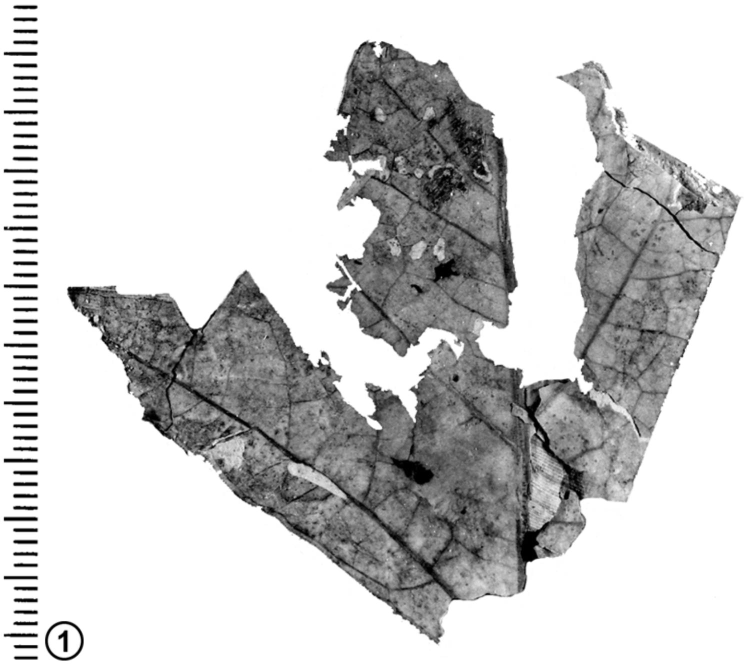
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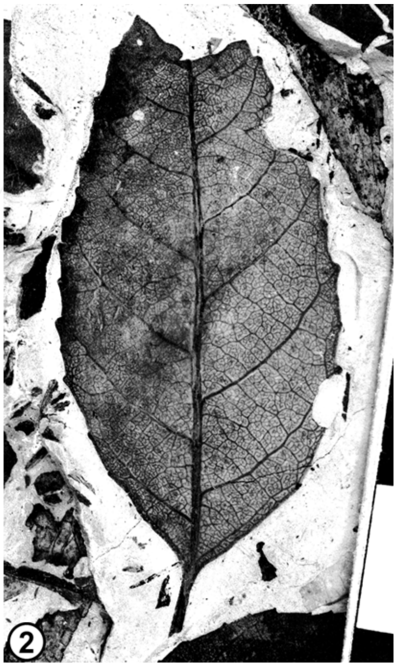
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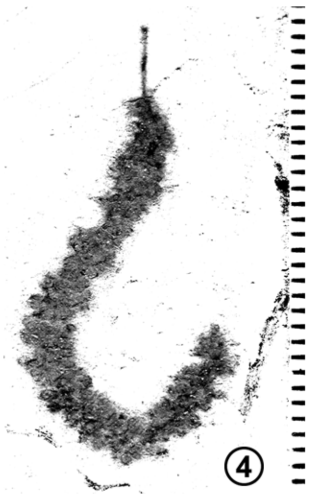
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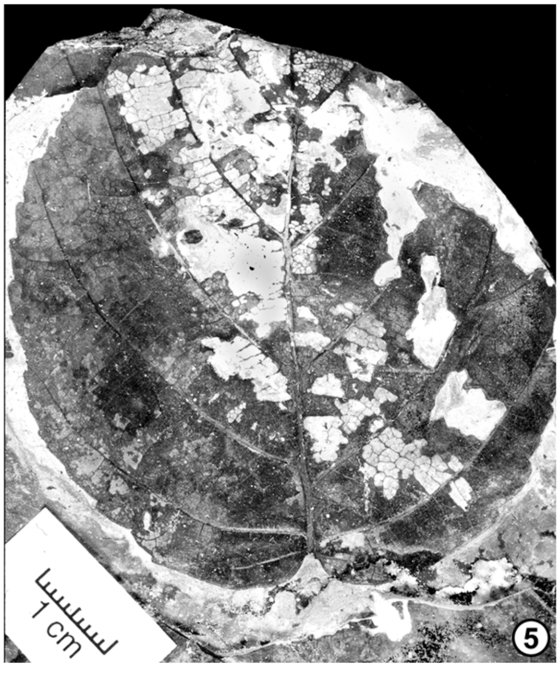

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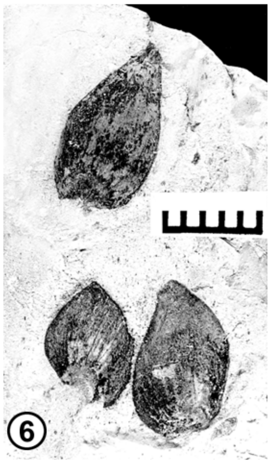
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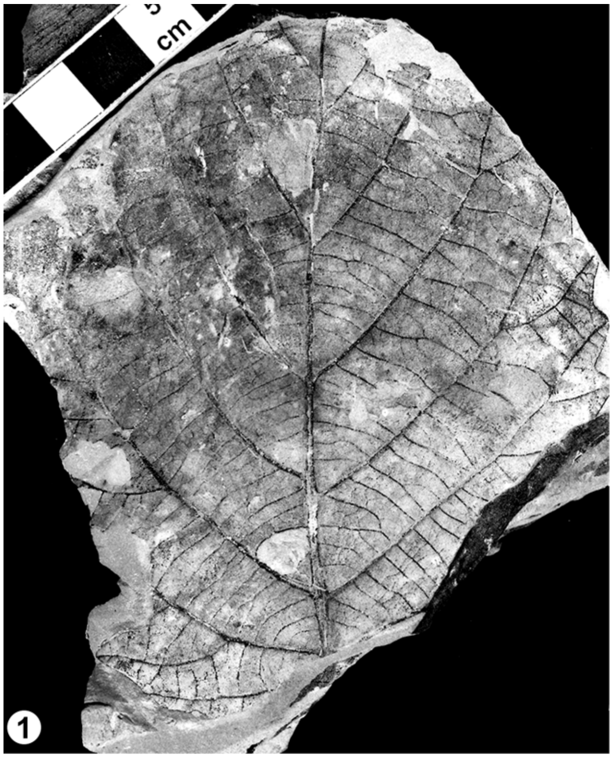
PLATE 7



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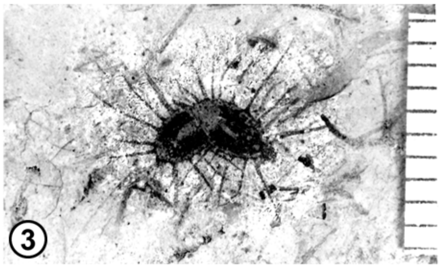

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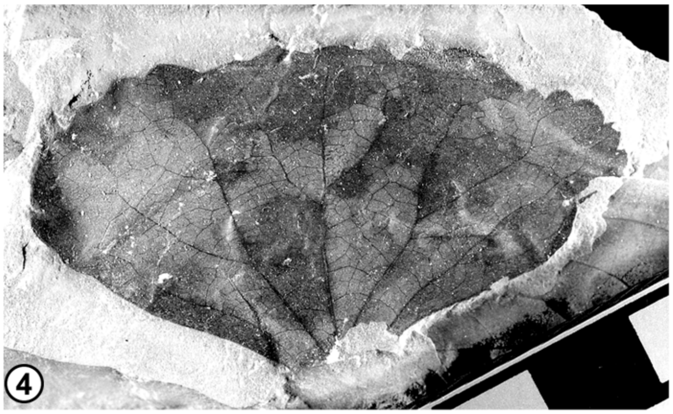

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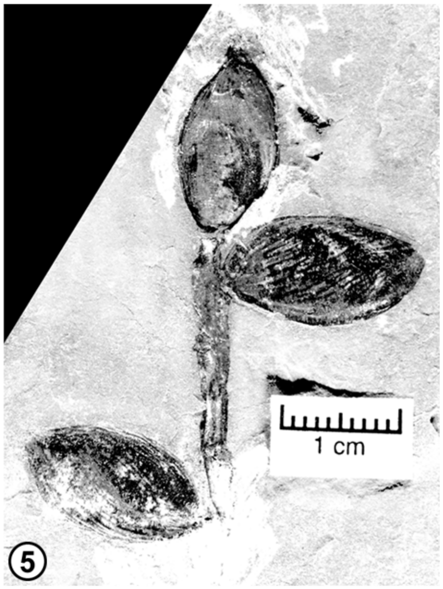

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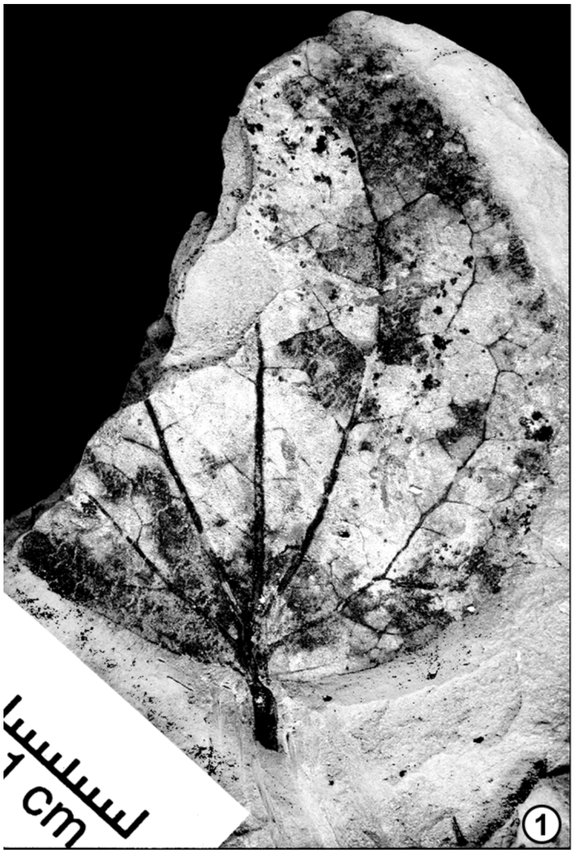

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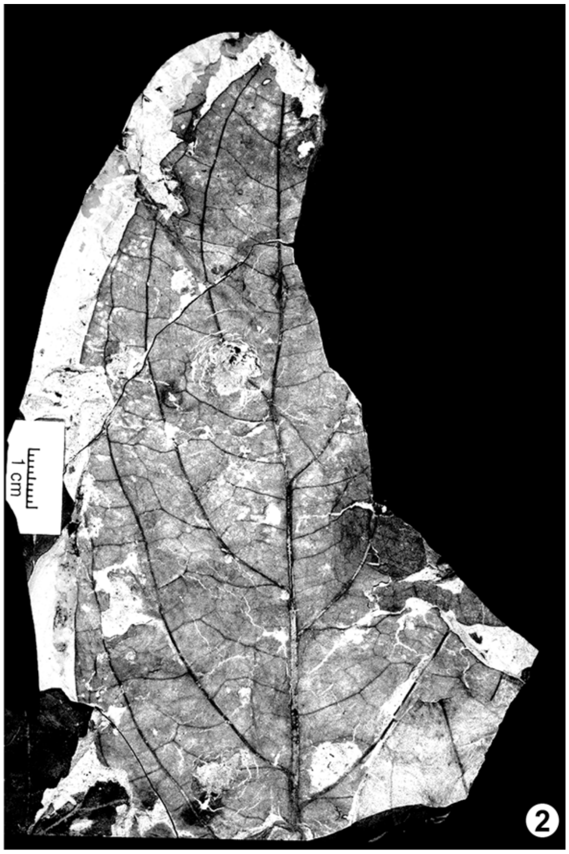

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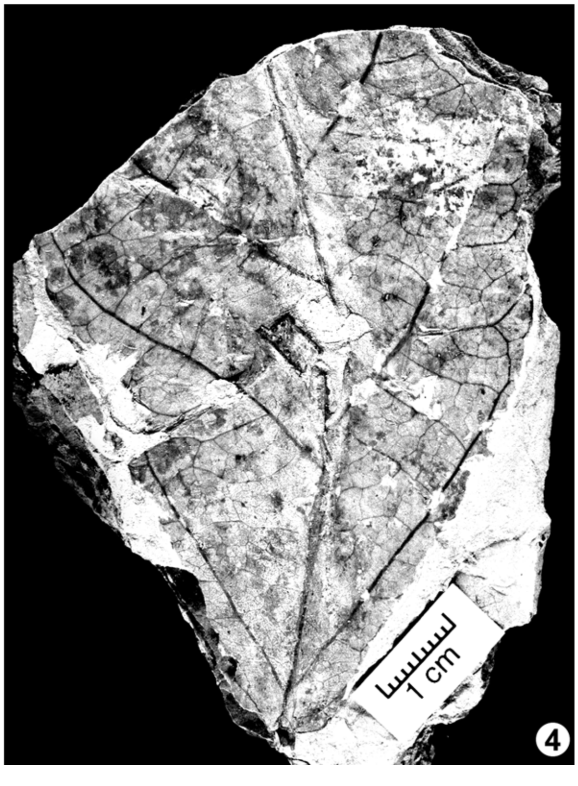

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PLATE 9


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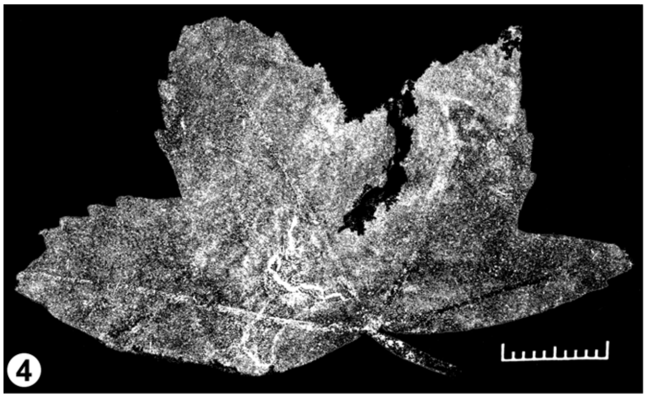
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PLATE 10


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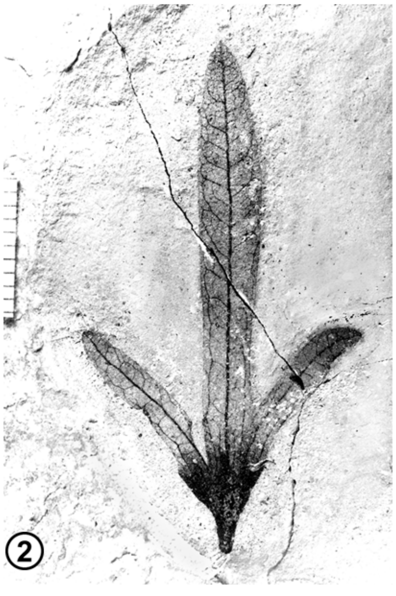
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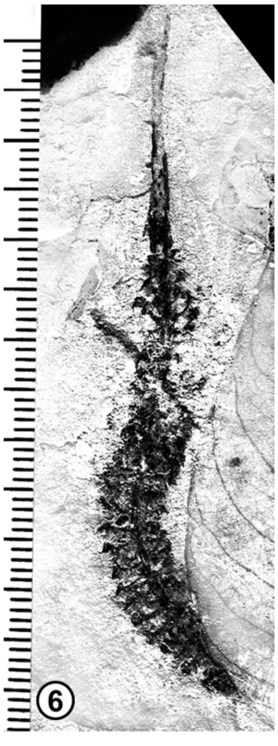
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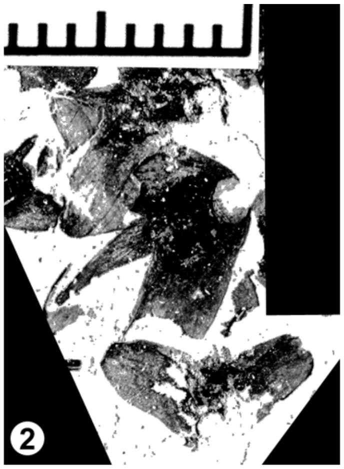
PLATE 11


①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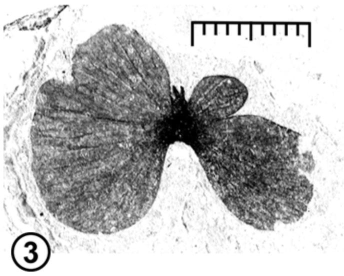
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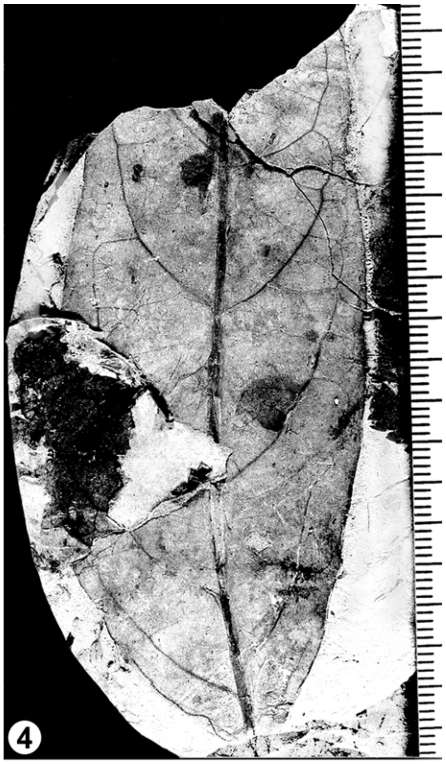
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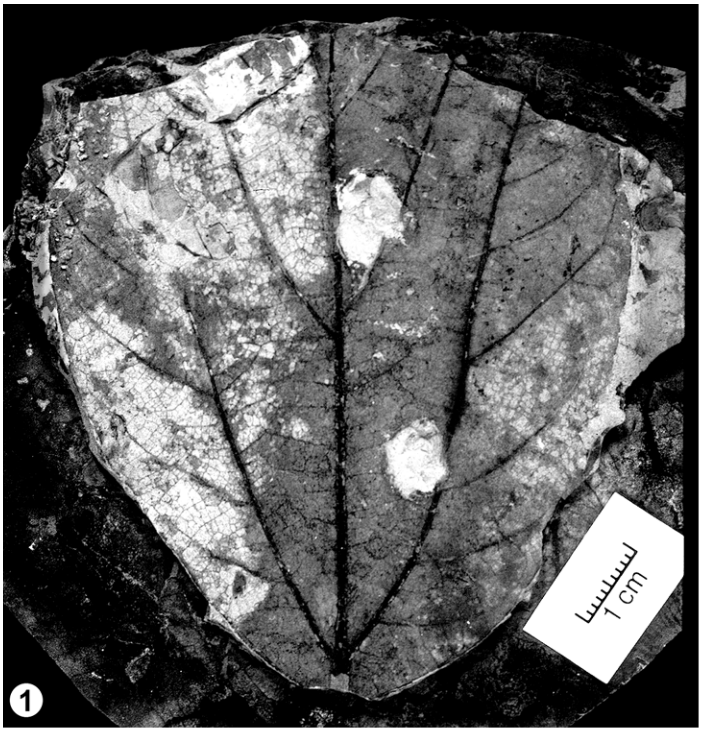
PLATE 12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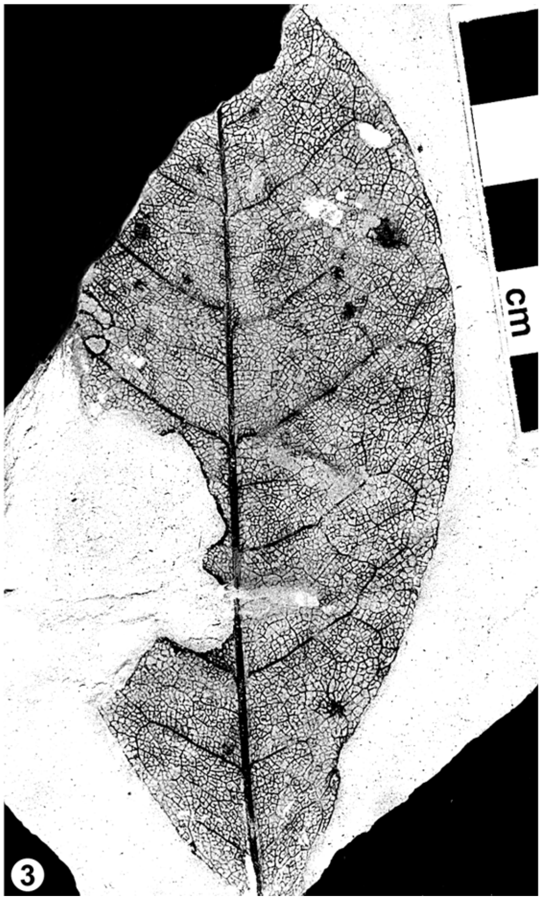
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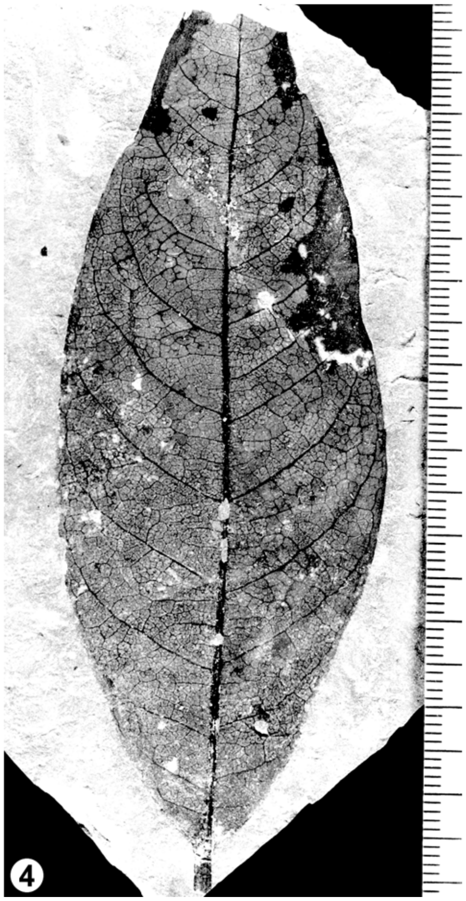
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PLATE 13


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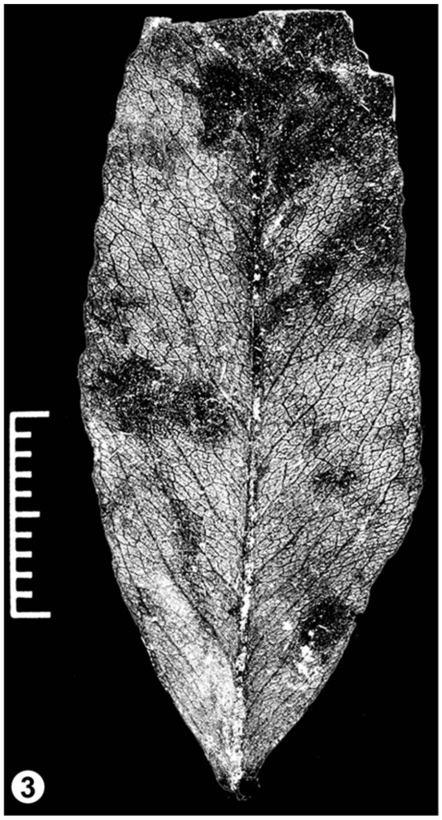
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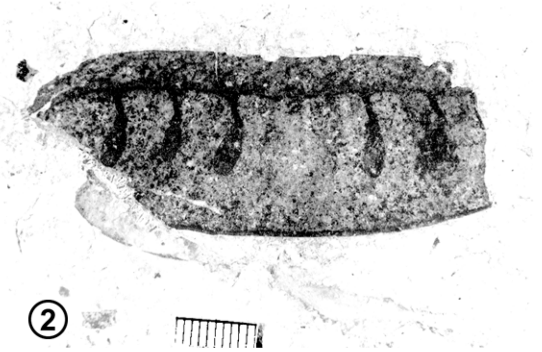
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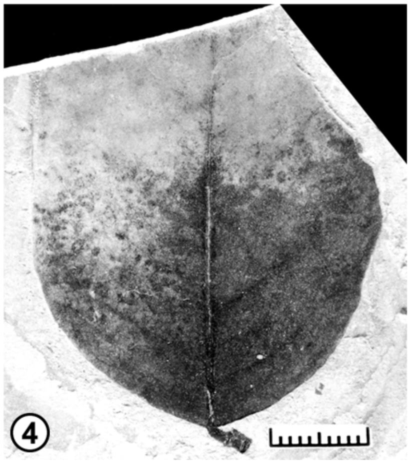
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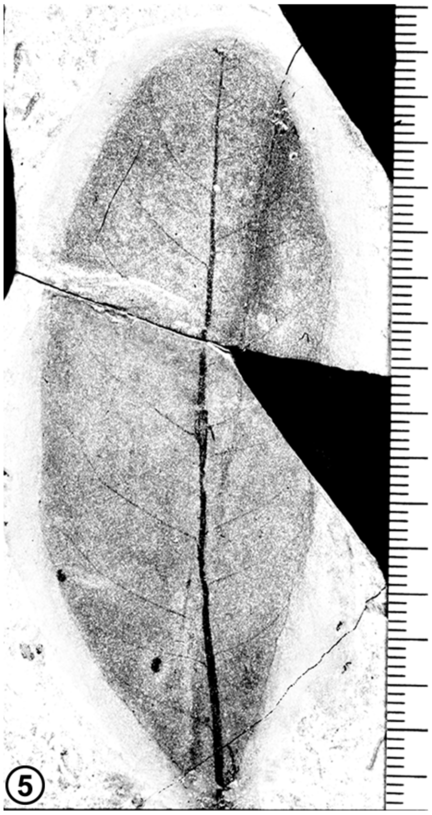
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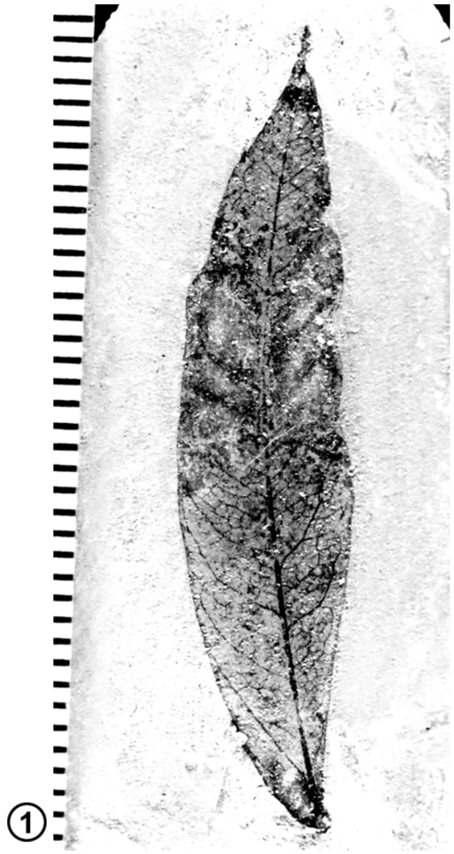
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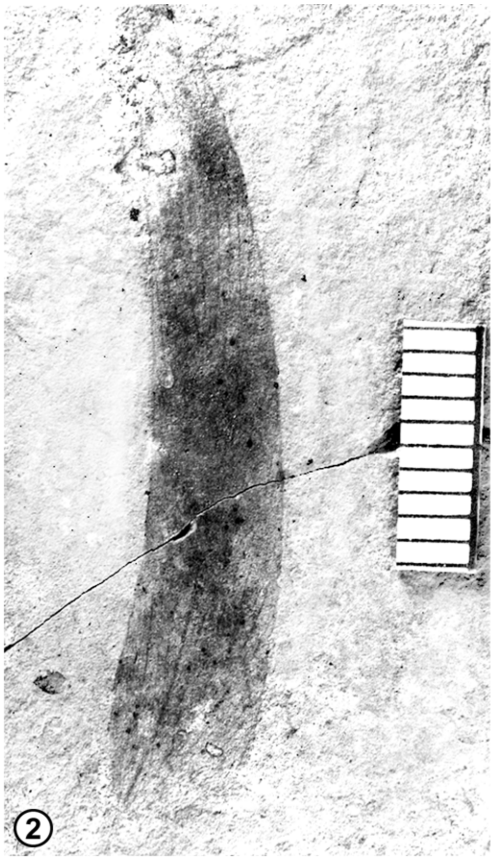
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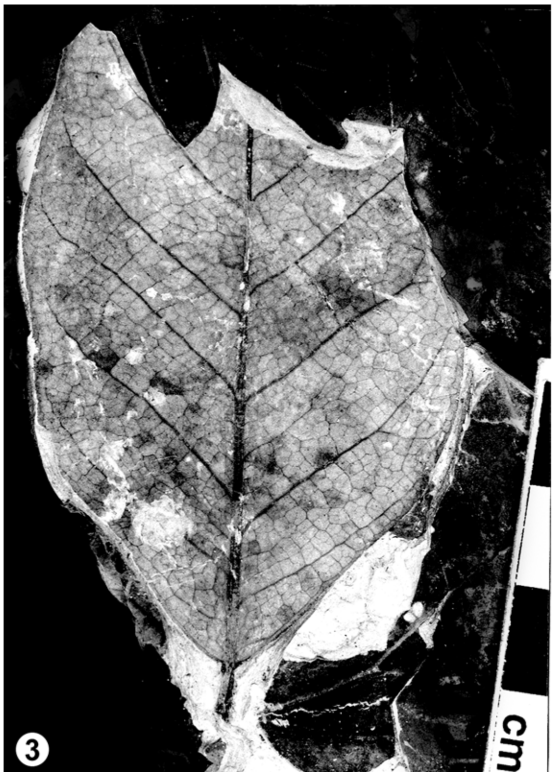
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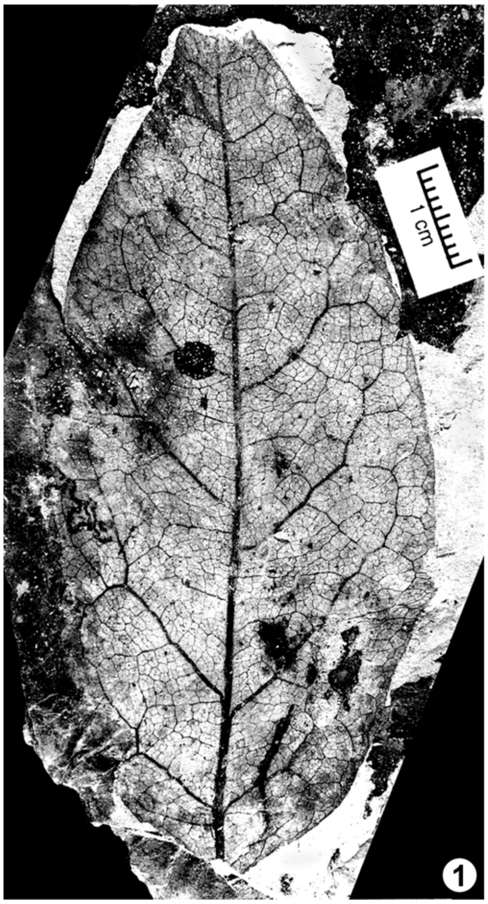
PLATE 15



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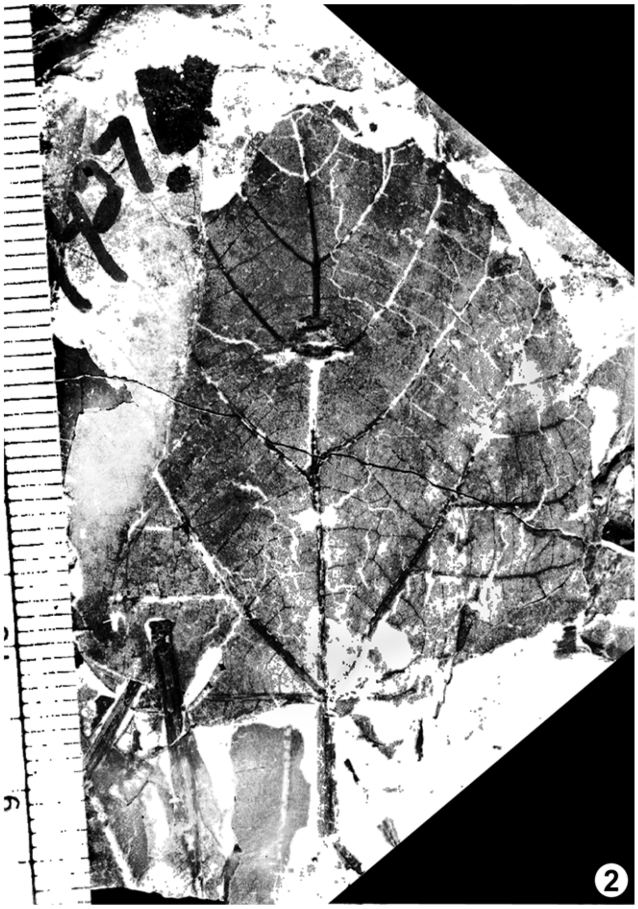

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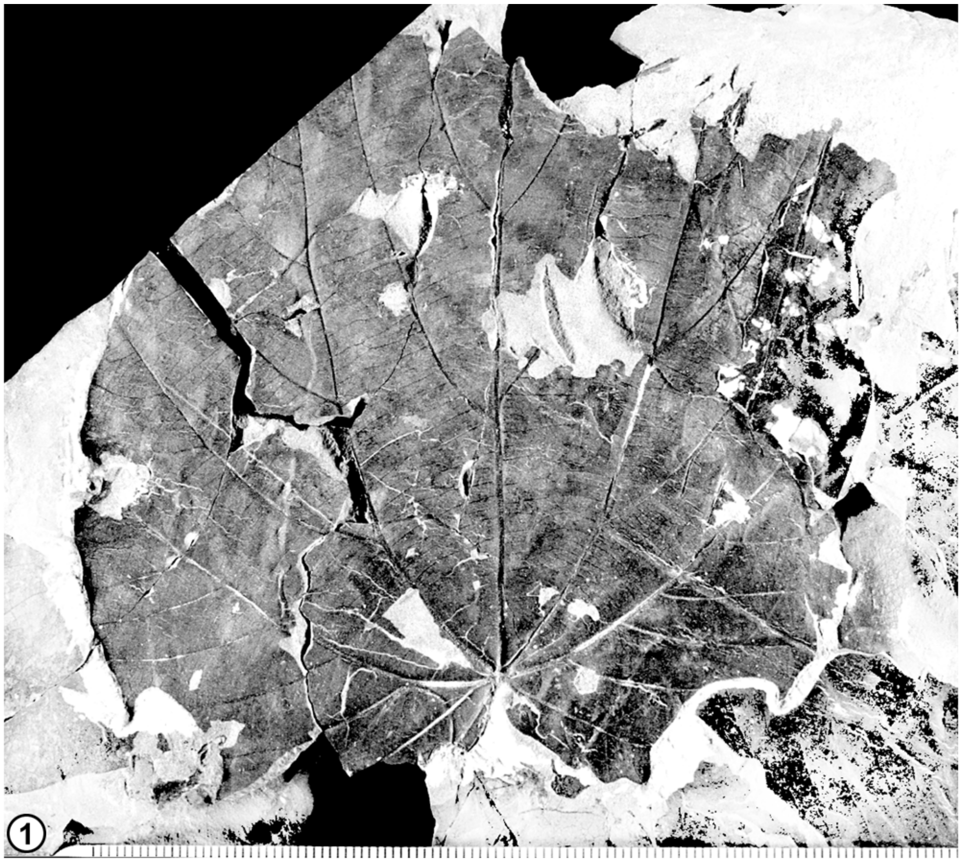
PLATE 16



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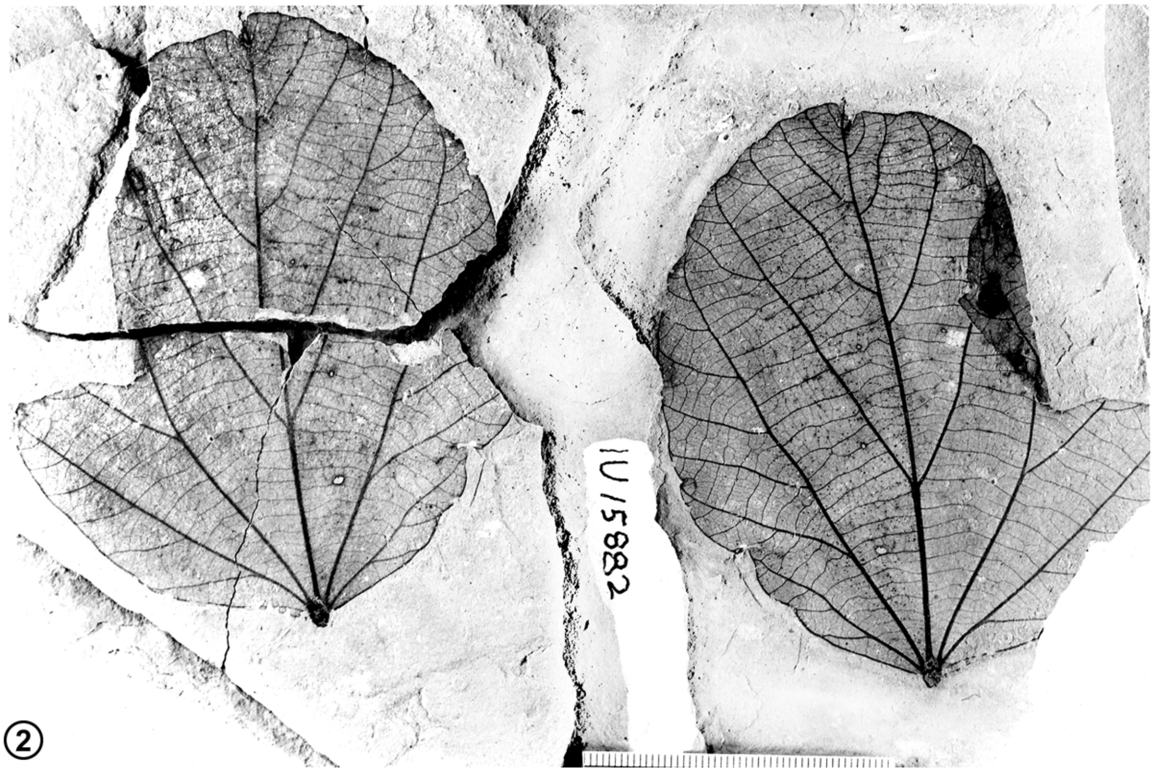

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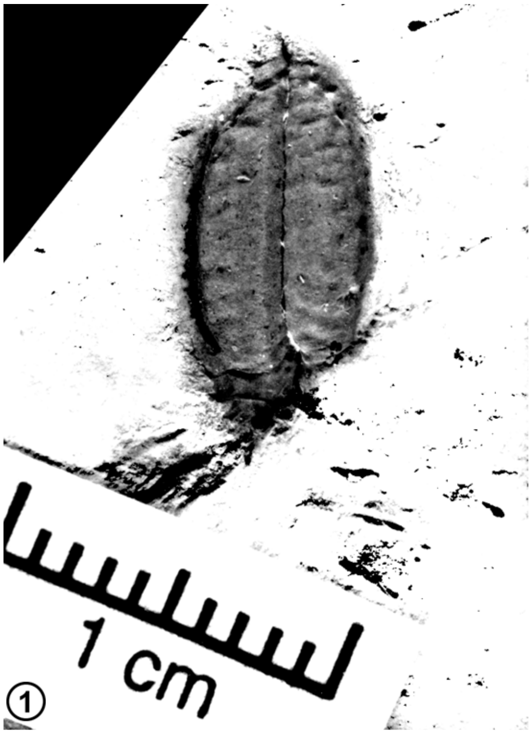
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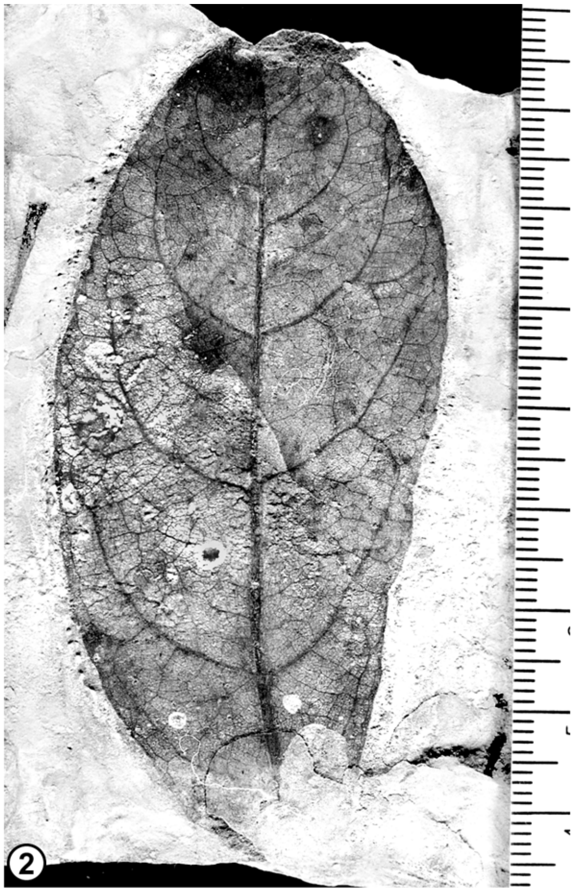
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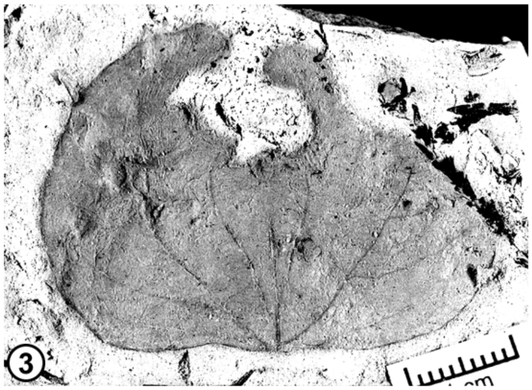
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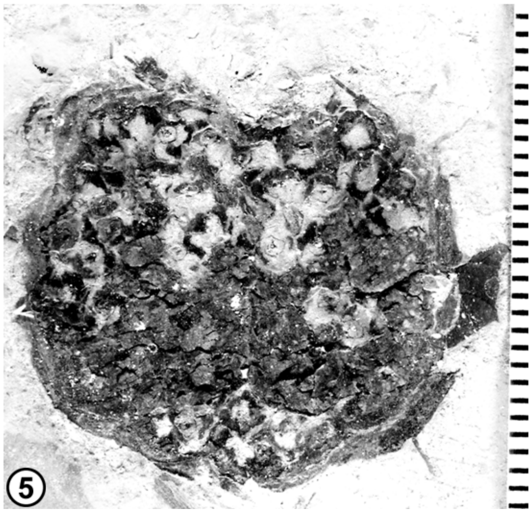
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PLATE 18

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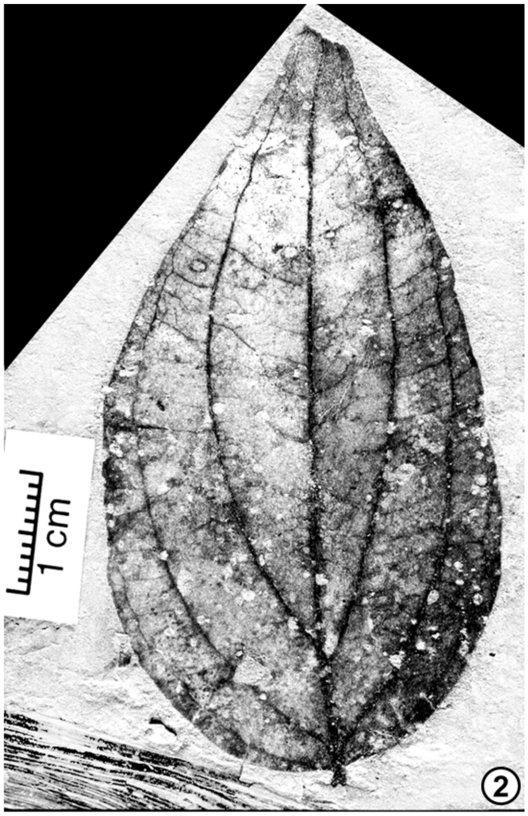

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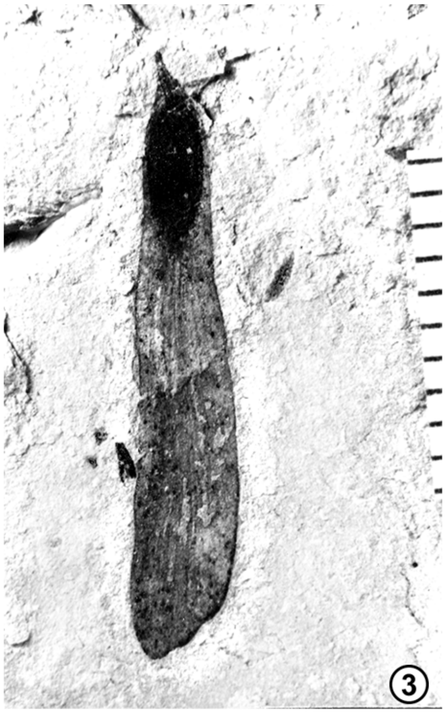

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PLATE 19


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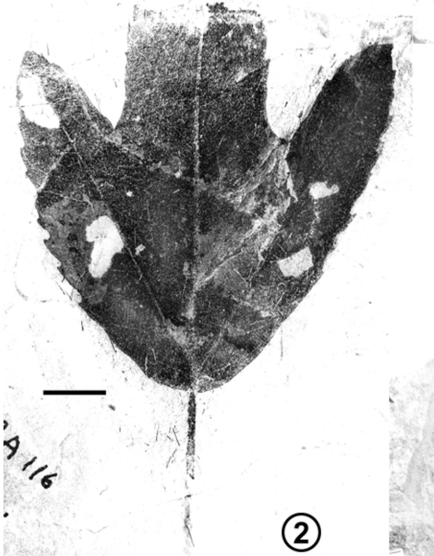
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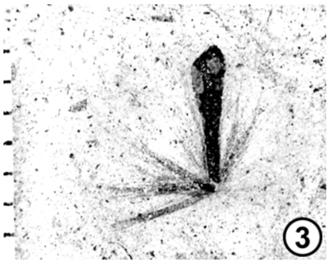
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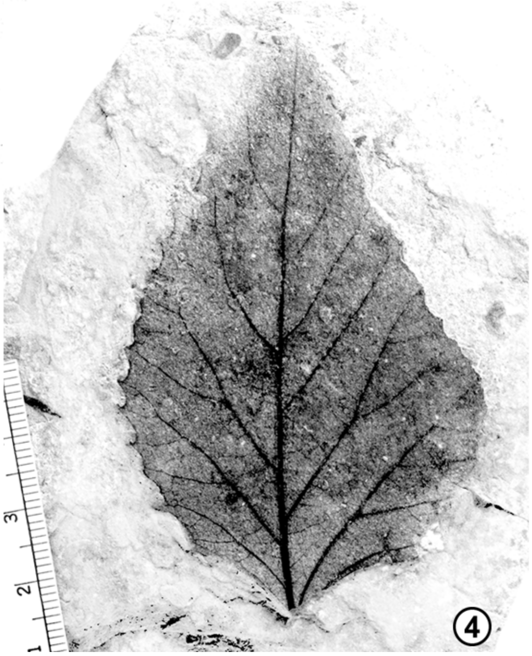
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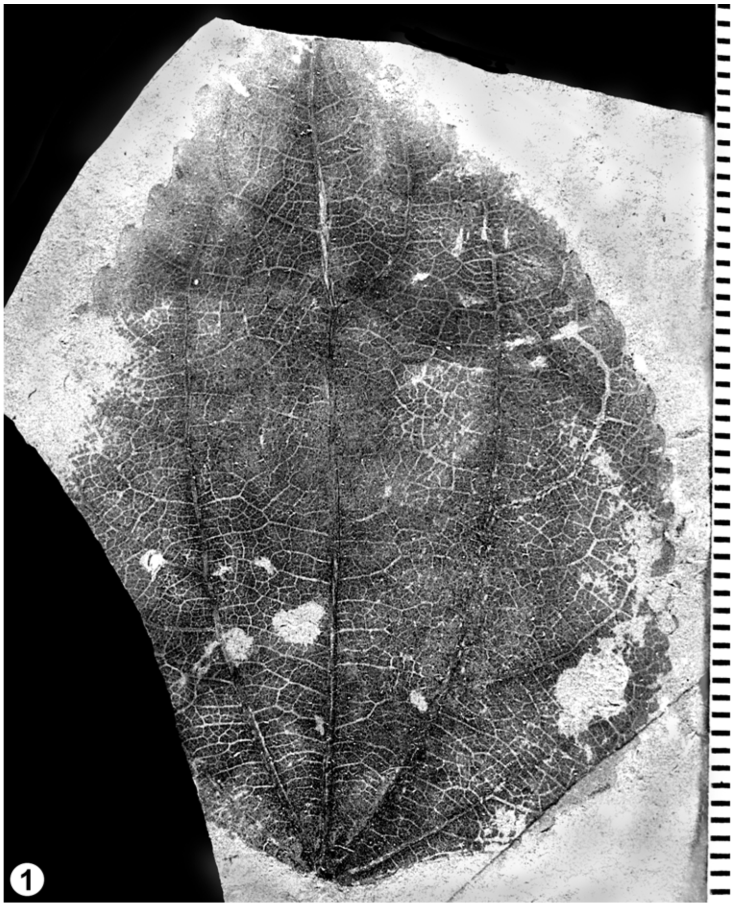
PLATE 20



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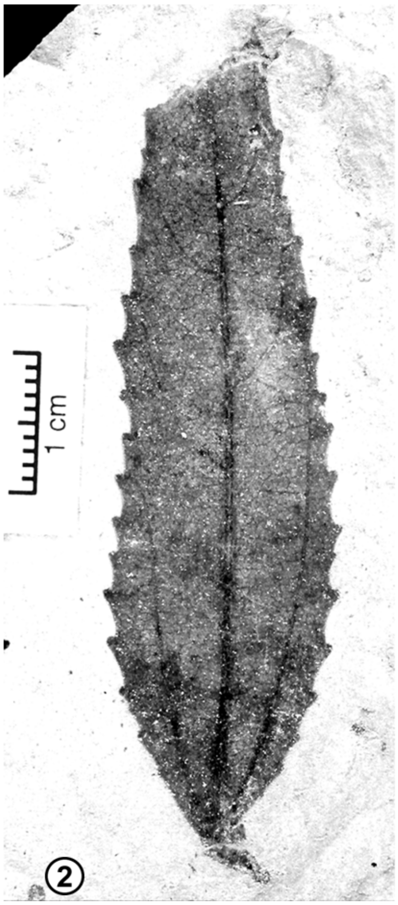

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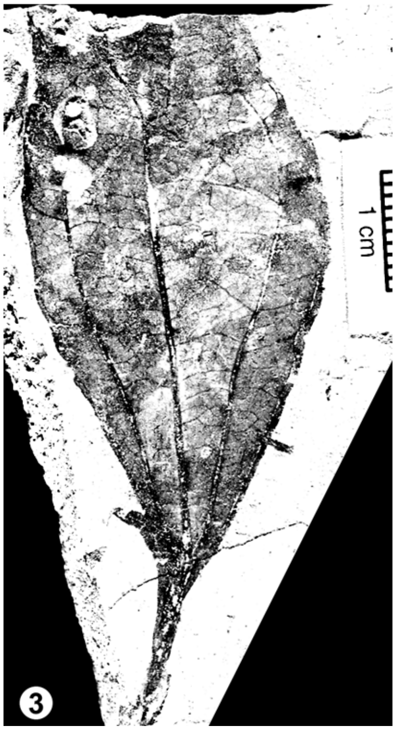

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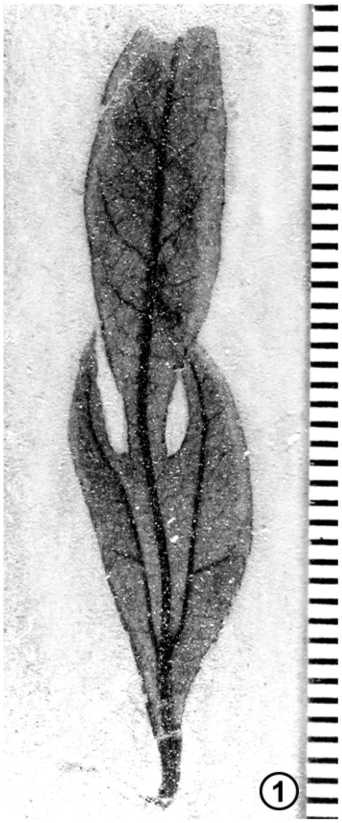
PLATE 21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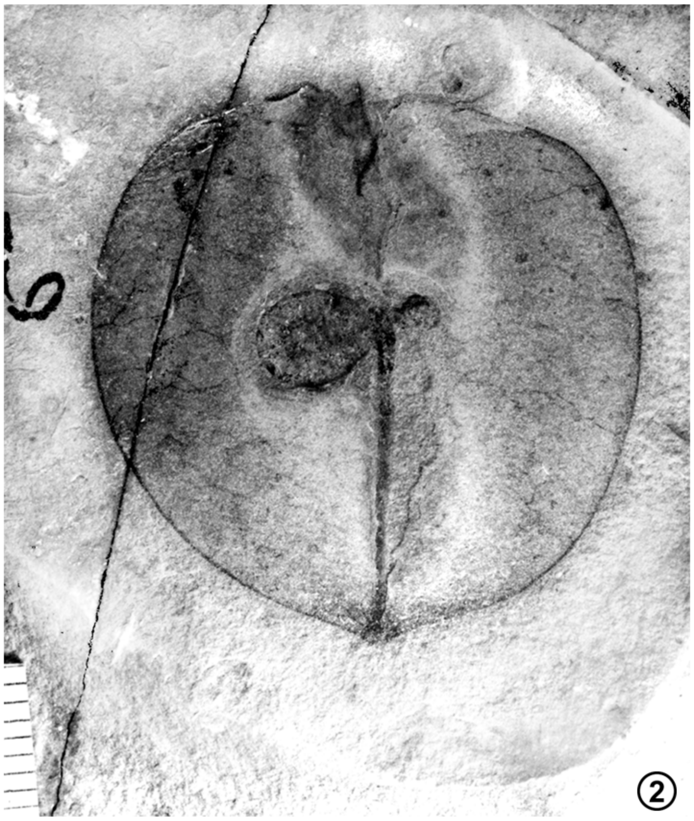
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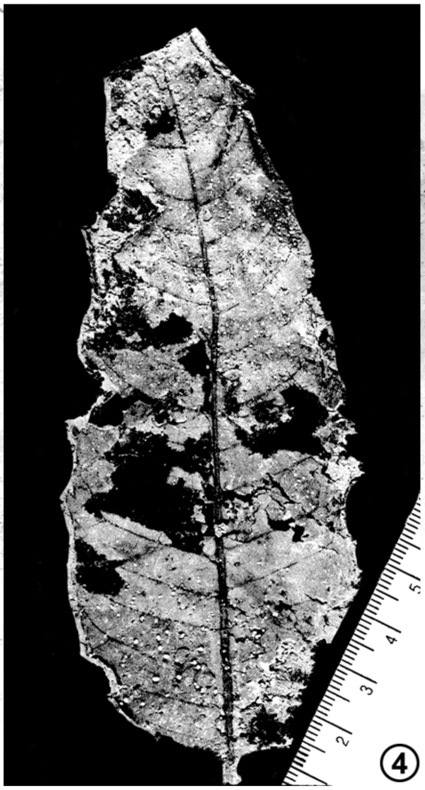

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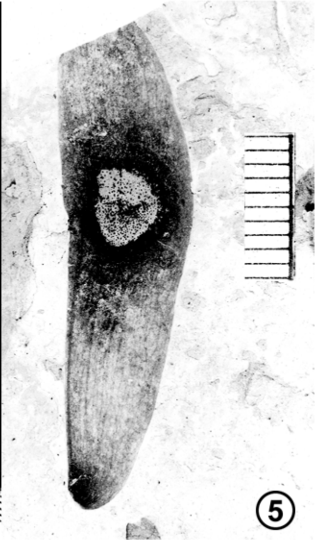
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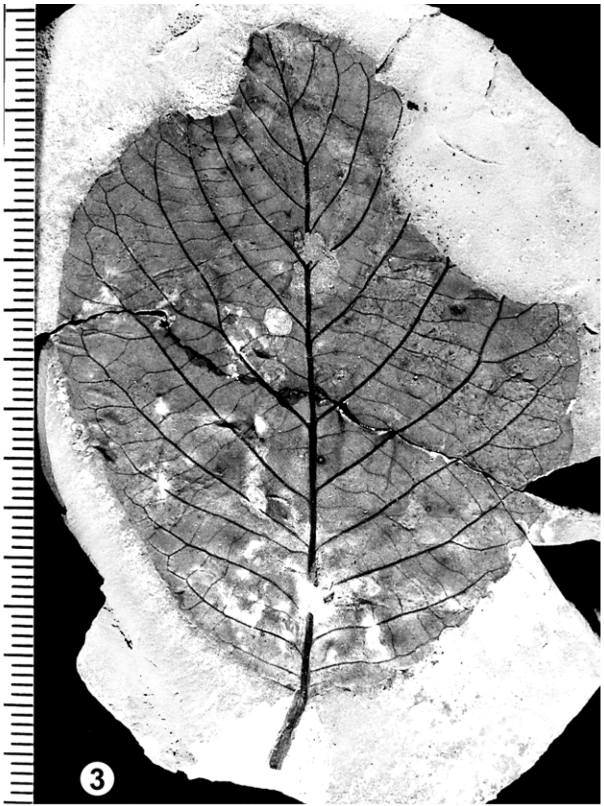
PLATE 22


①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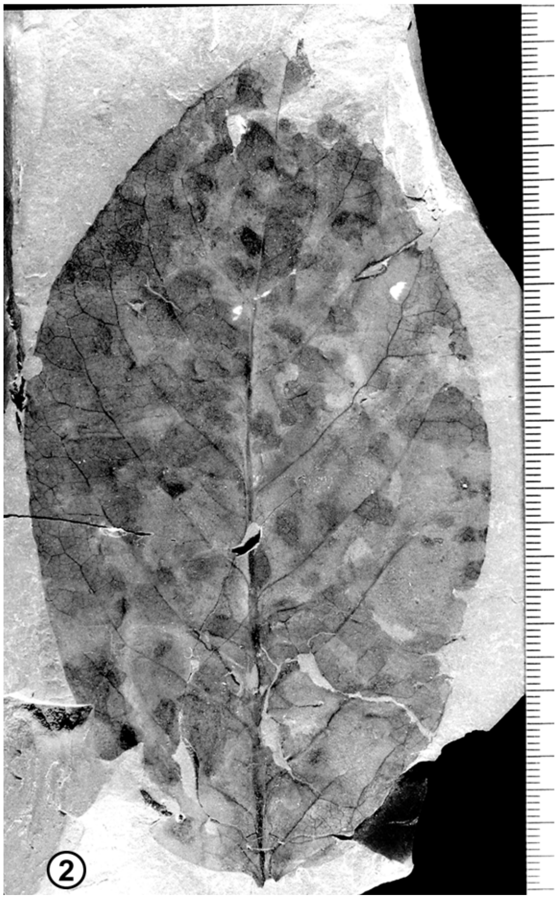
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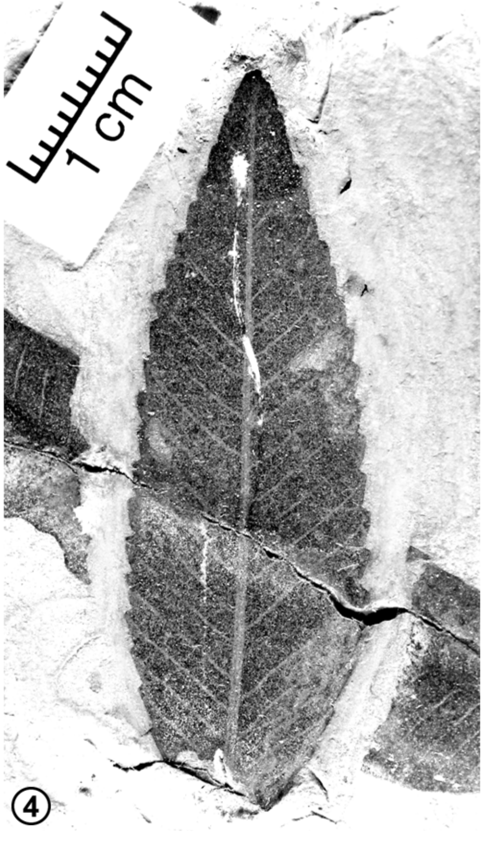
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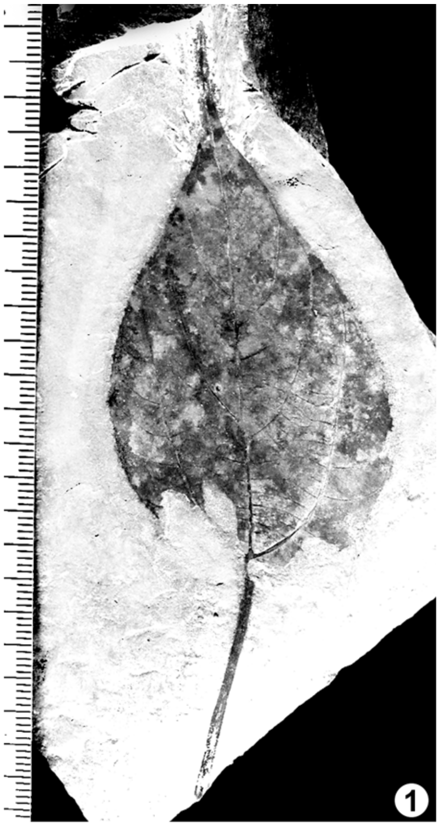

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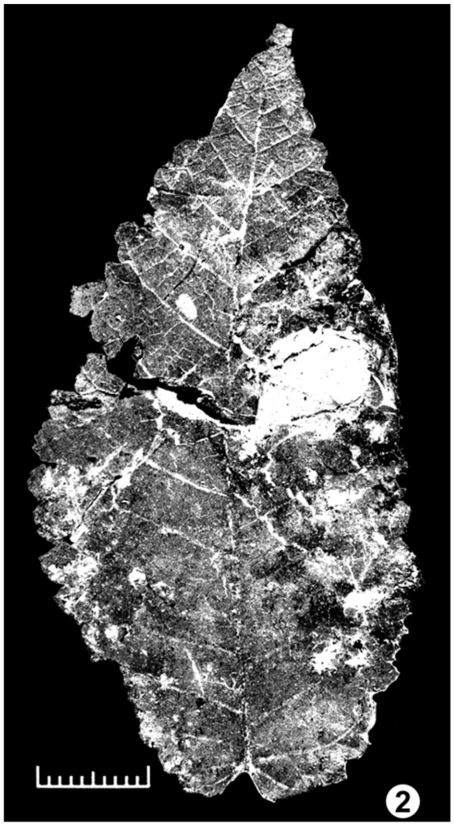

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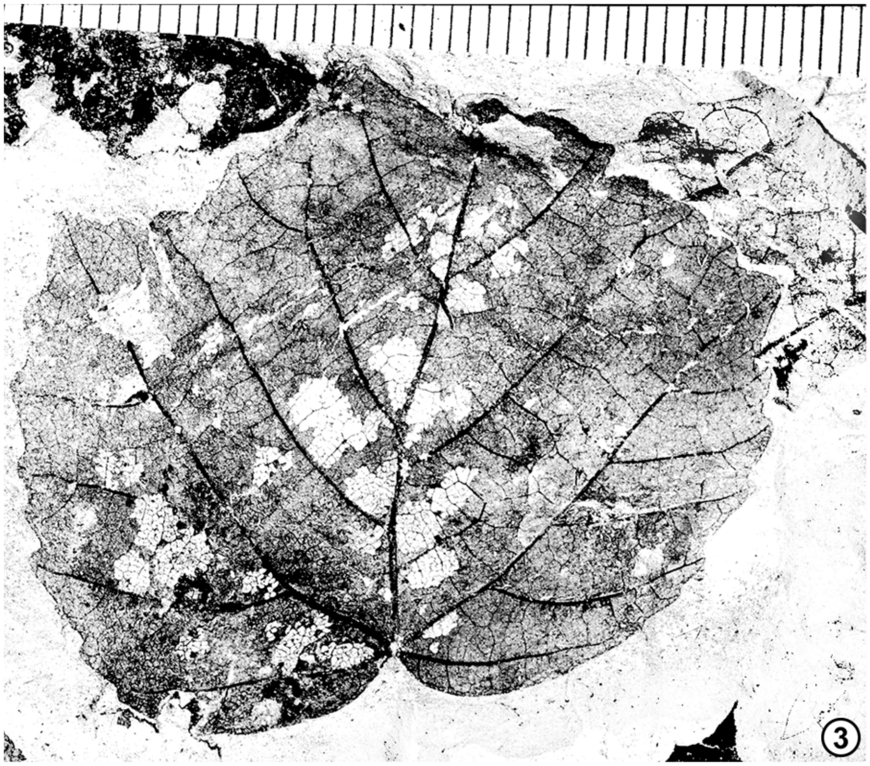
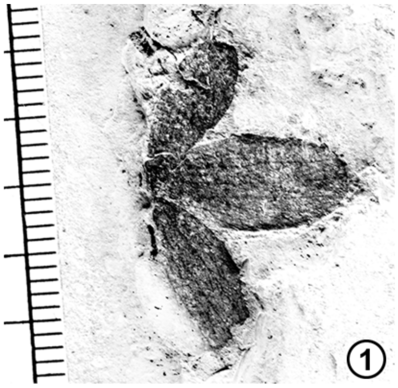


3

PLATE 24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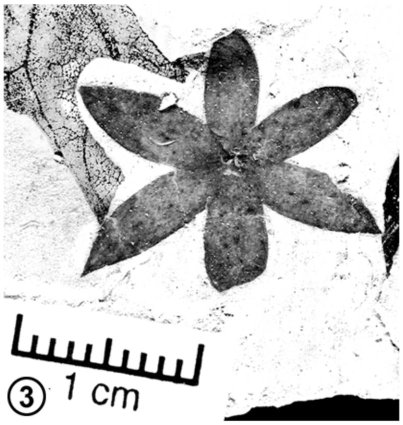
②


③


④

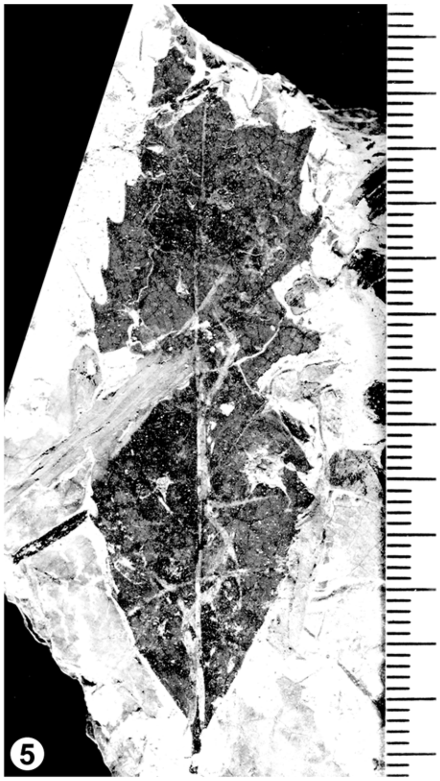

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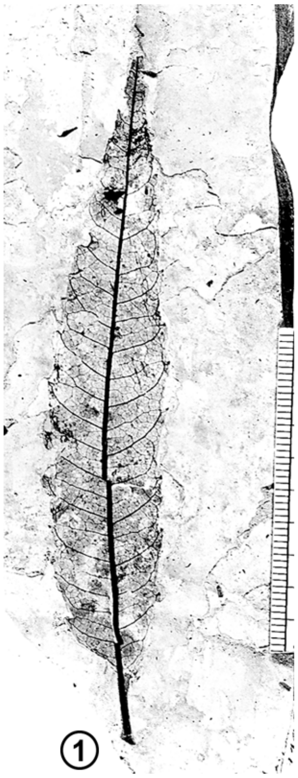
PLATE 25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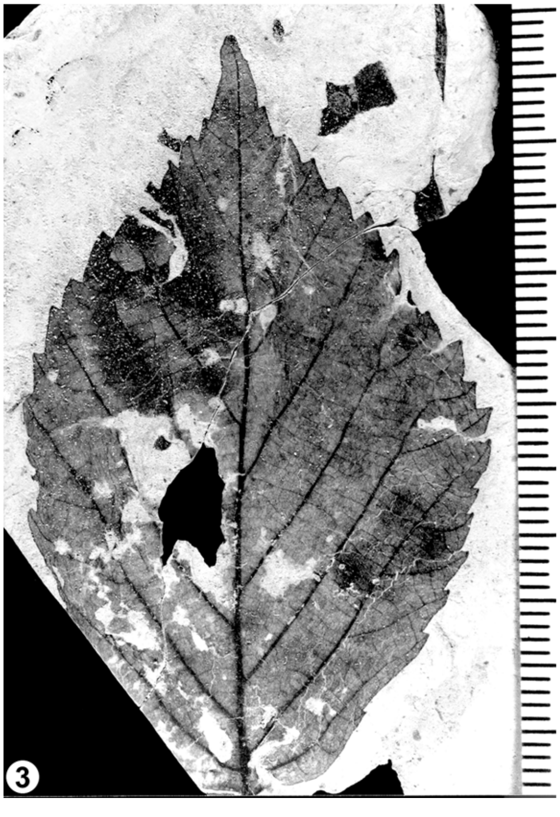
②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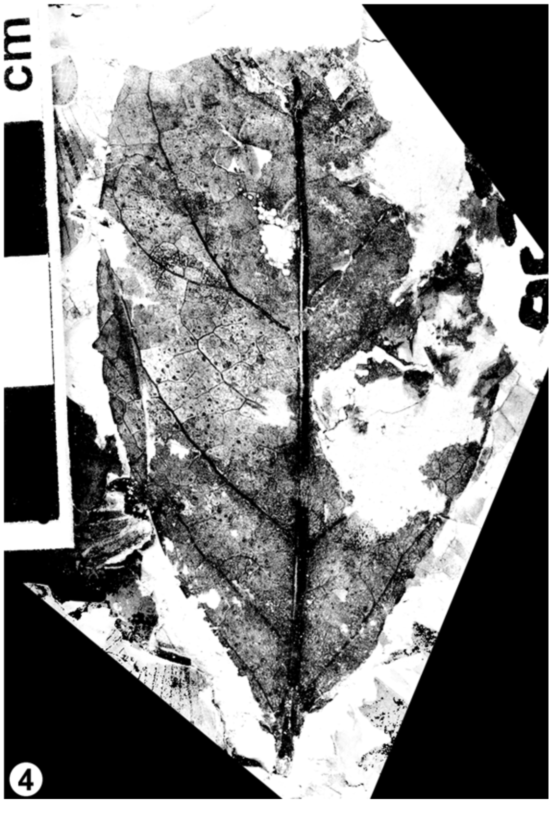
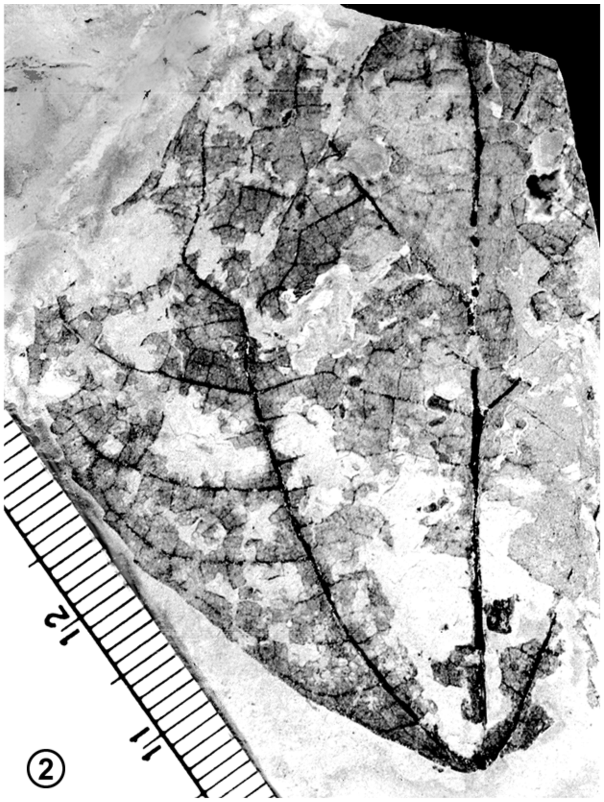


④

PLATE 26



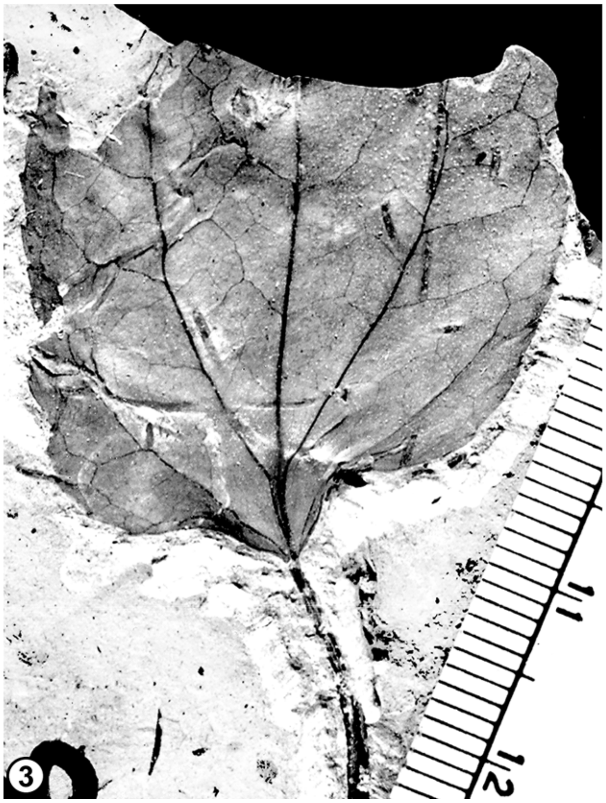
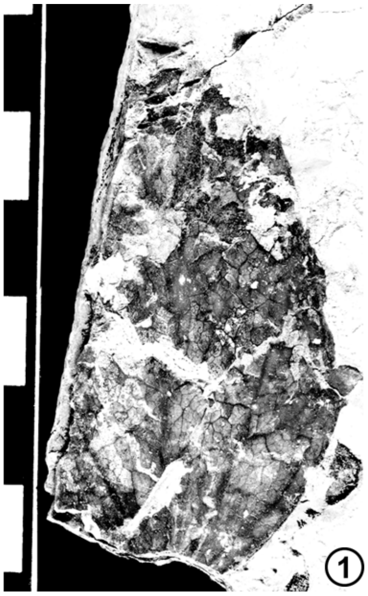
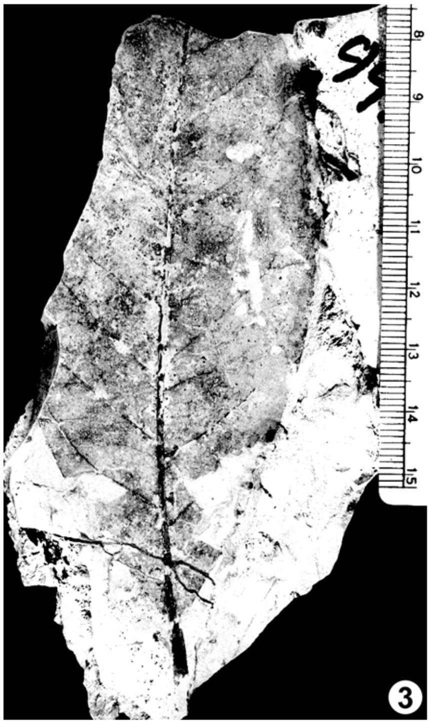
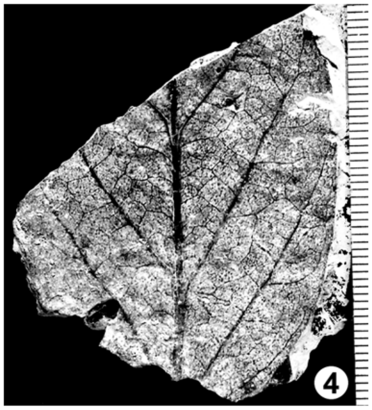


PLATE 27







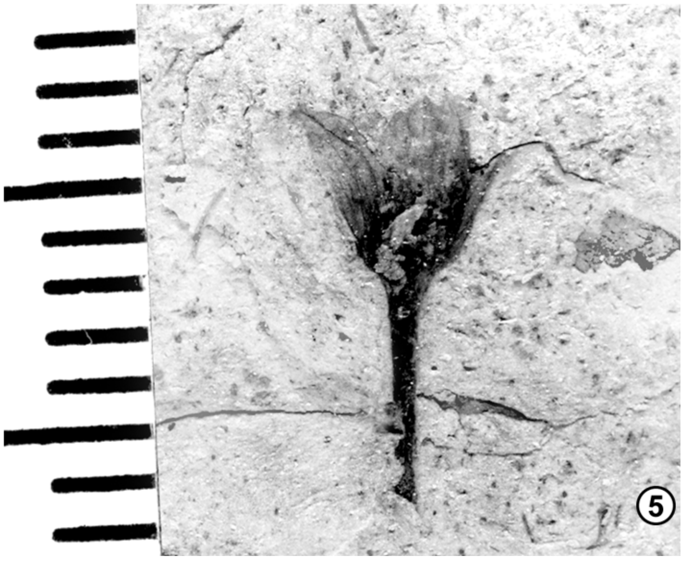
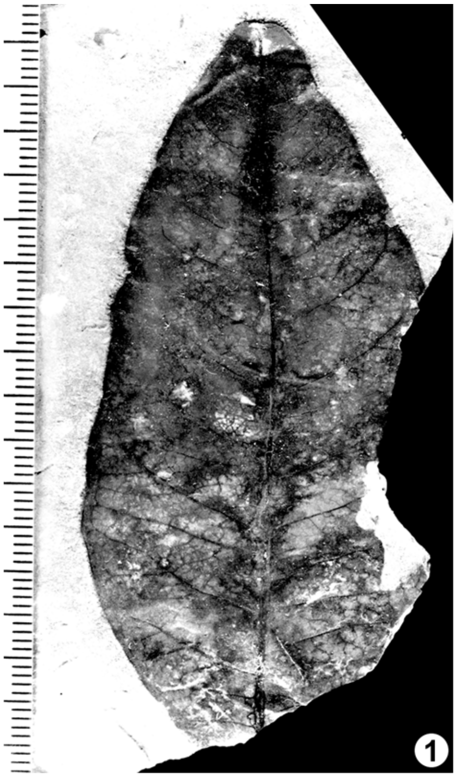
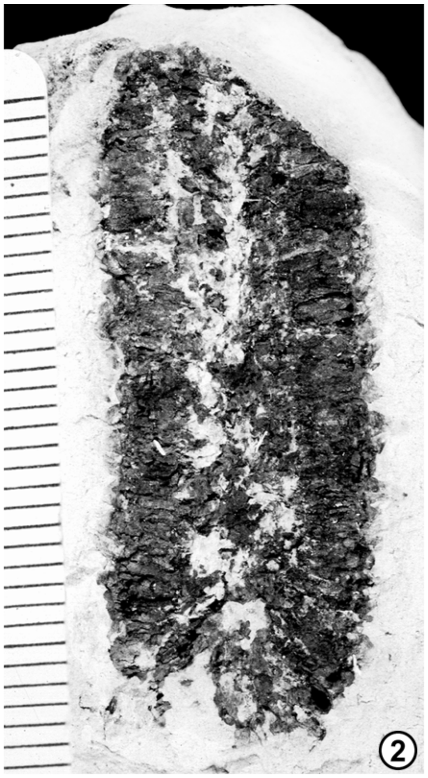
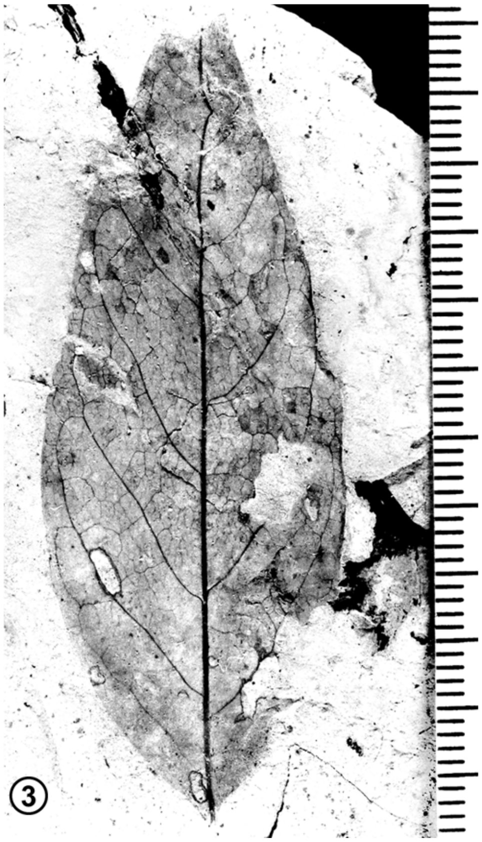


PLATE 28







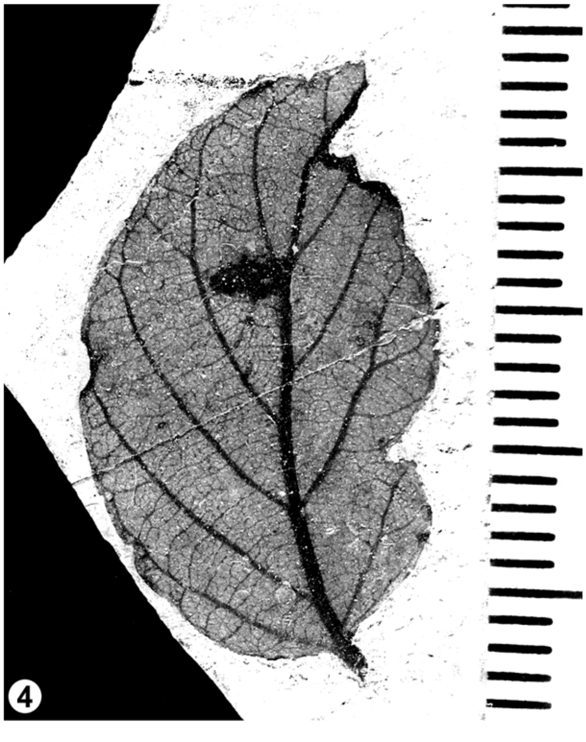
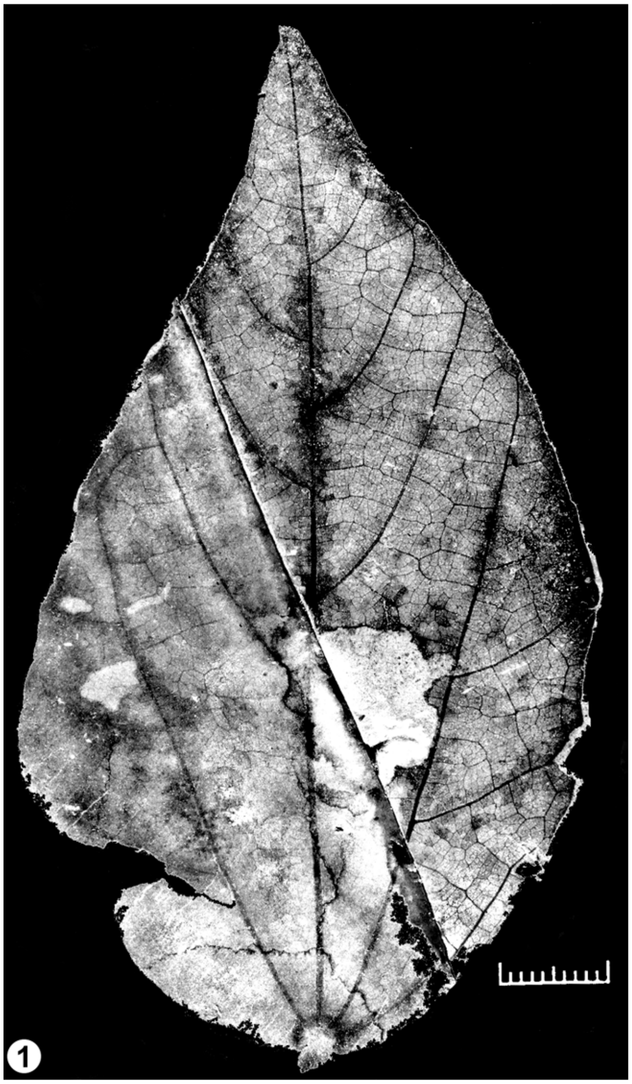


PLATE 29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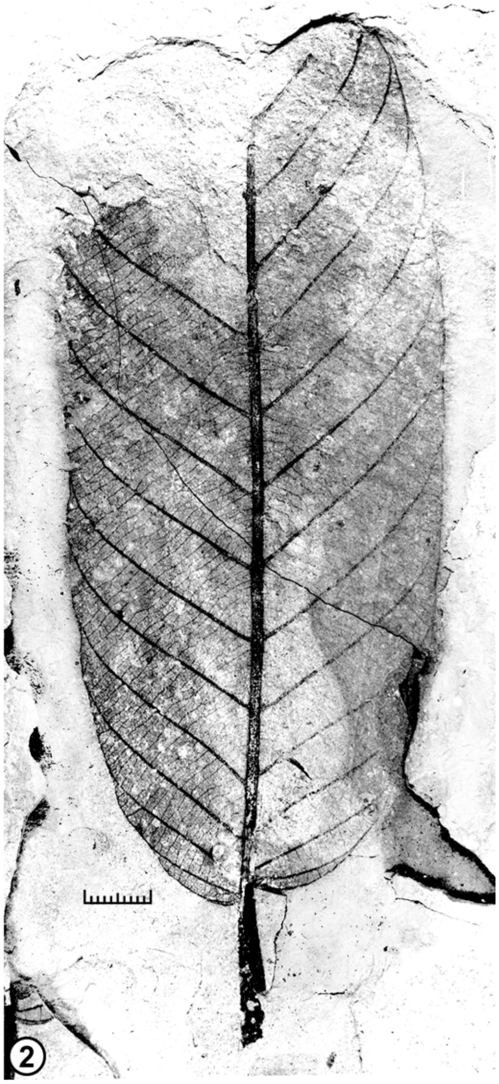
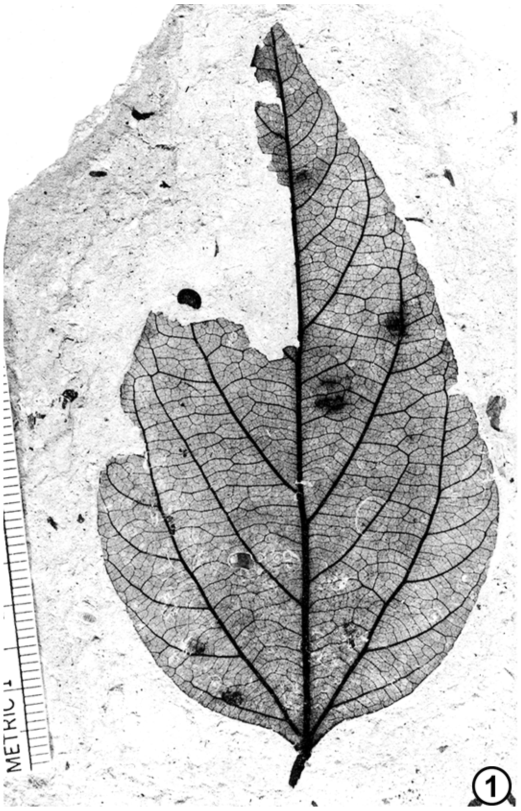

②

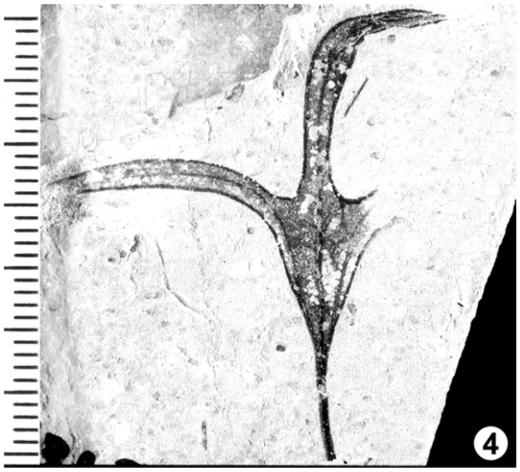
PLATE 30



①


②


③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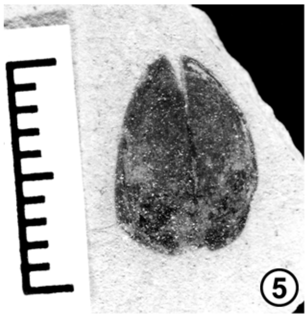
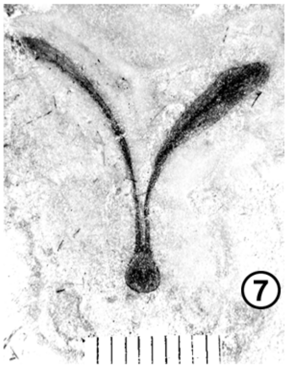
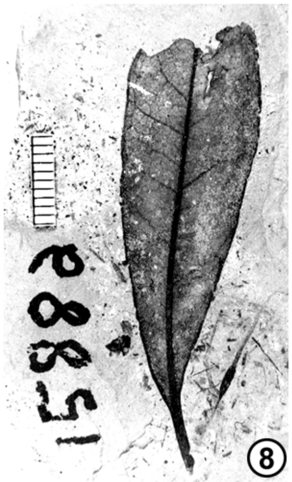

⑤


⑥


⑦



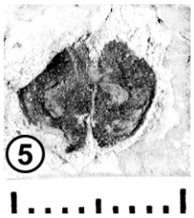
⑧

PLATE 31


1


2


3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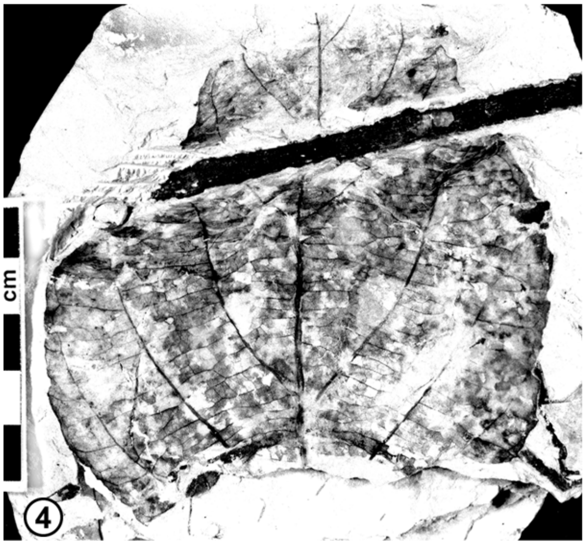
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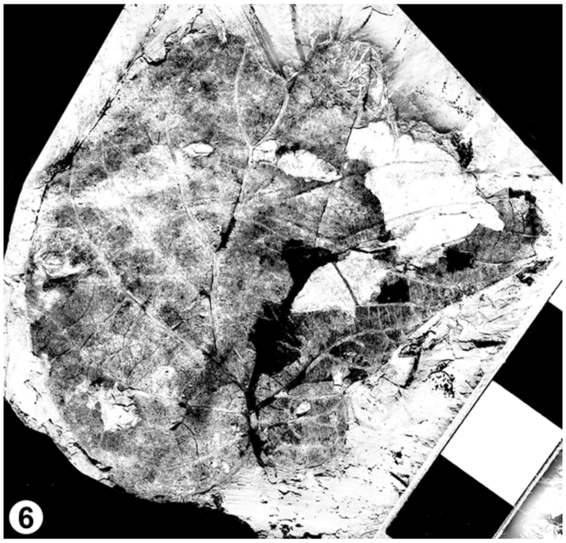
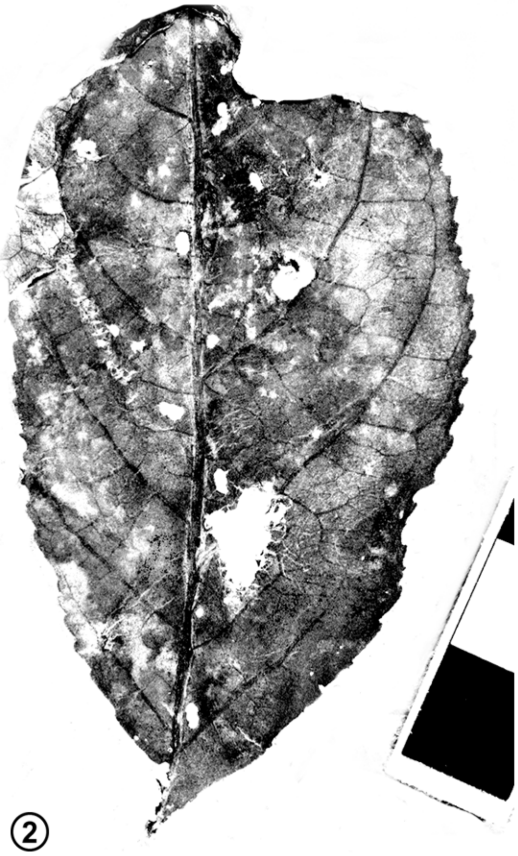

6

①



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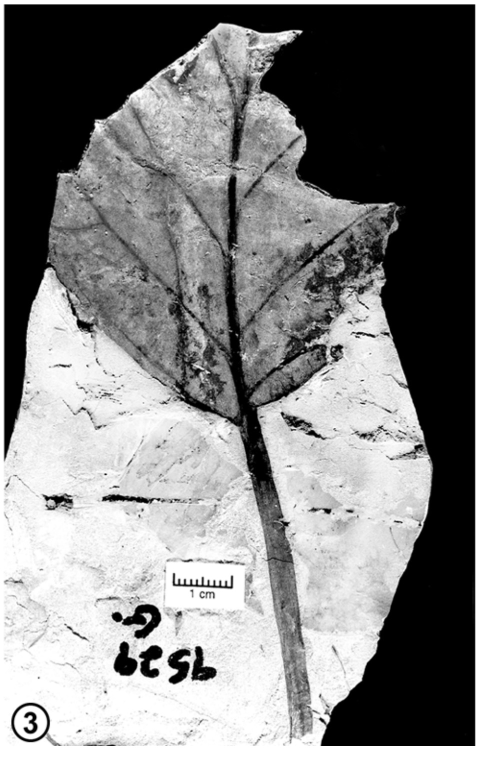

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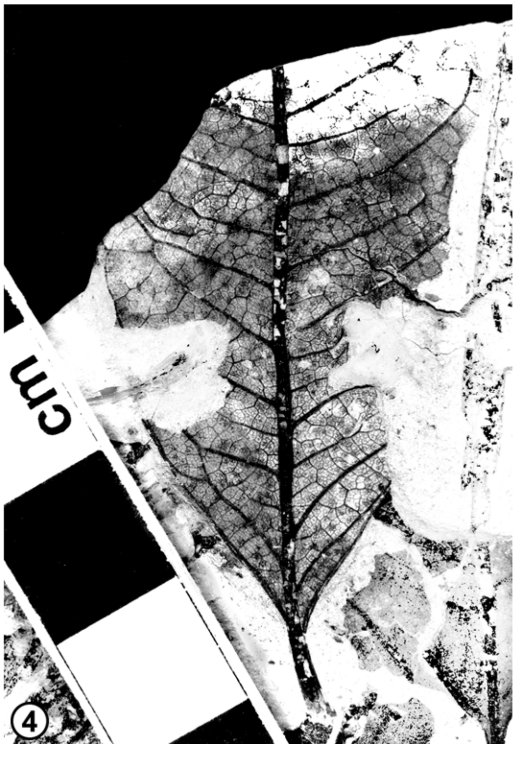
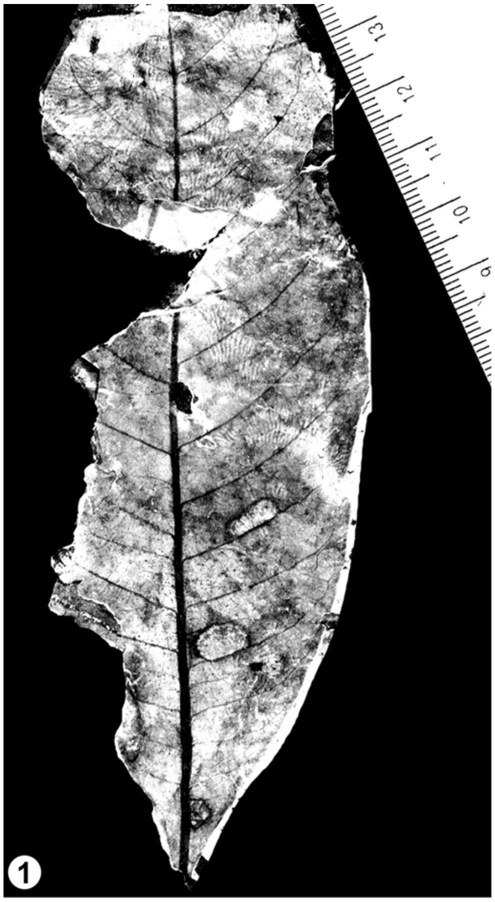


④

PLATE 33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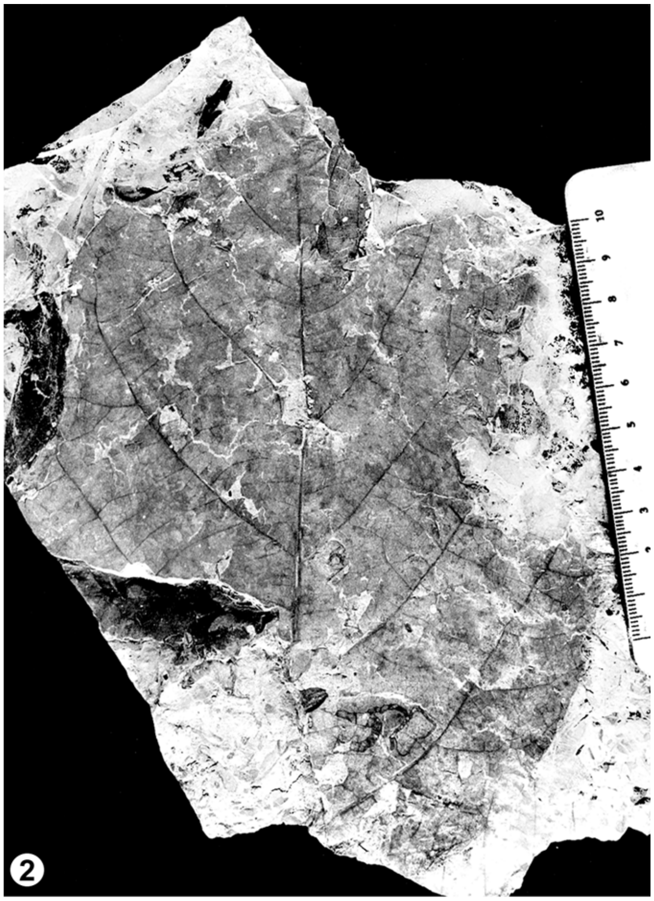
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3

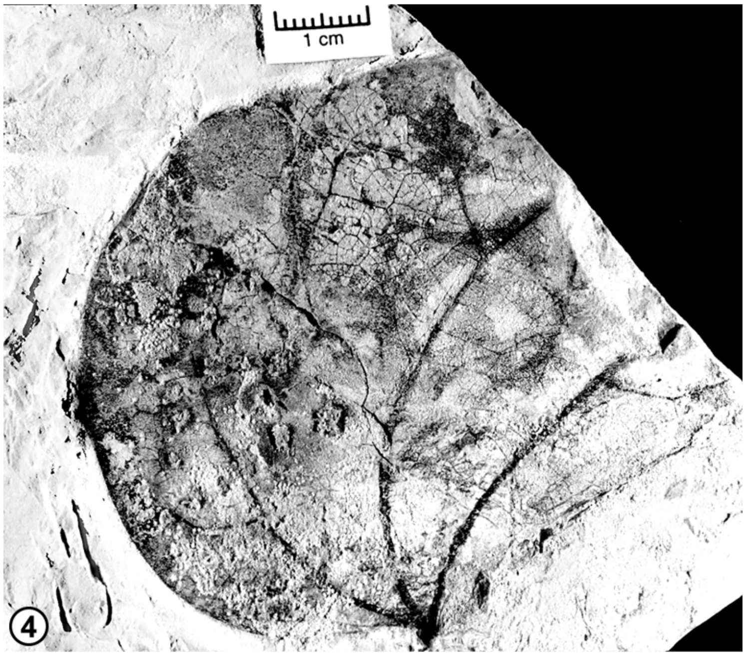
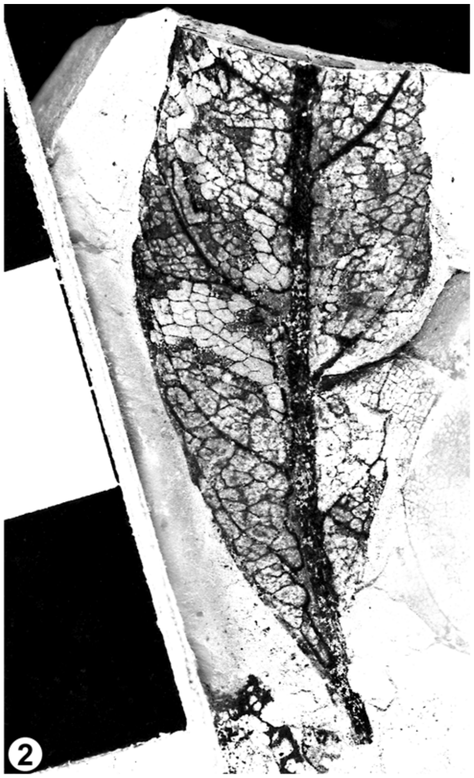
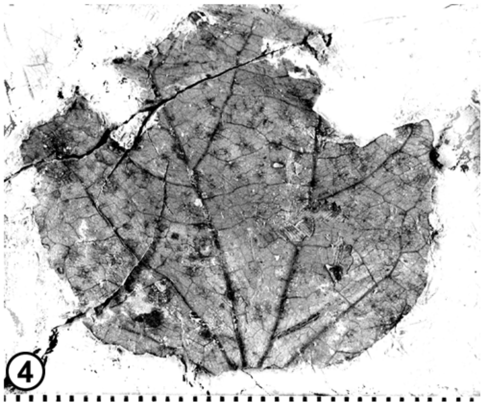

4

PLATE 34


①


②


③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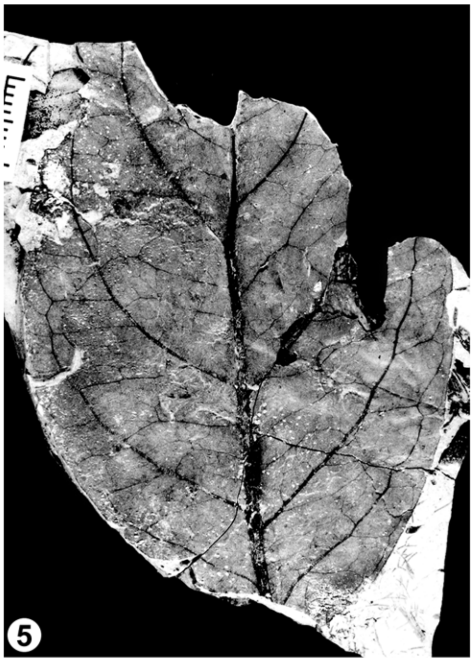
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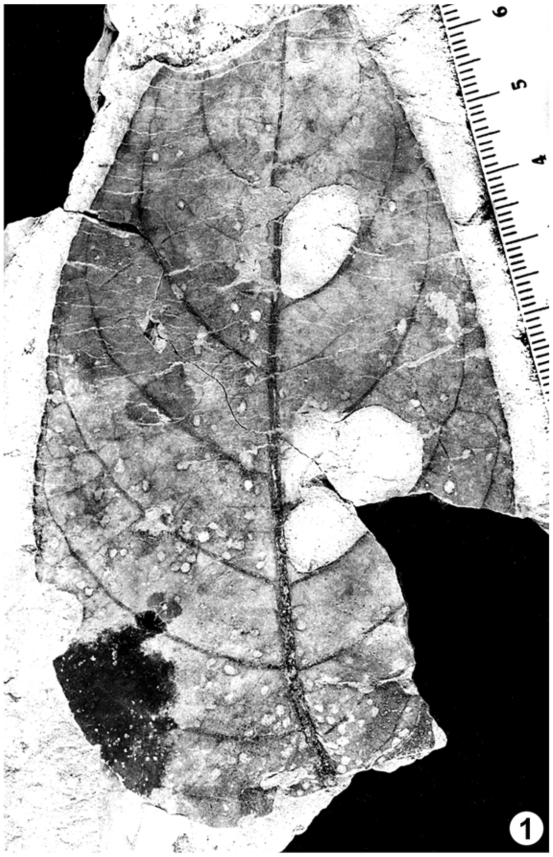

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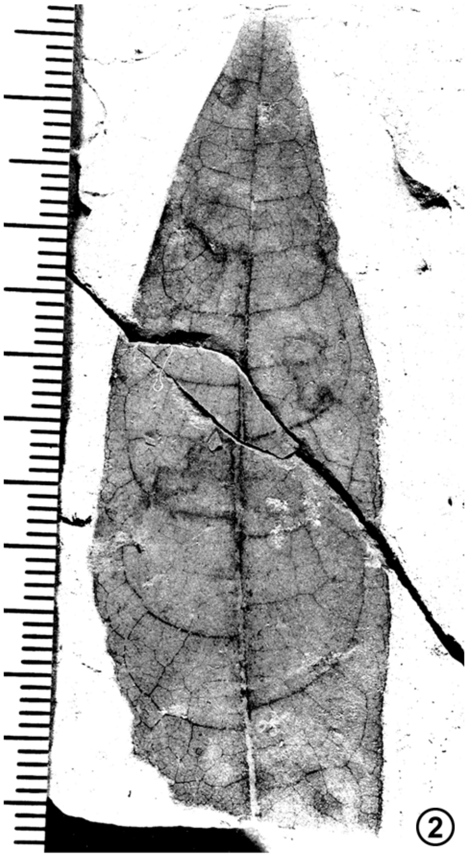

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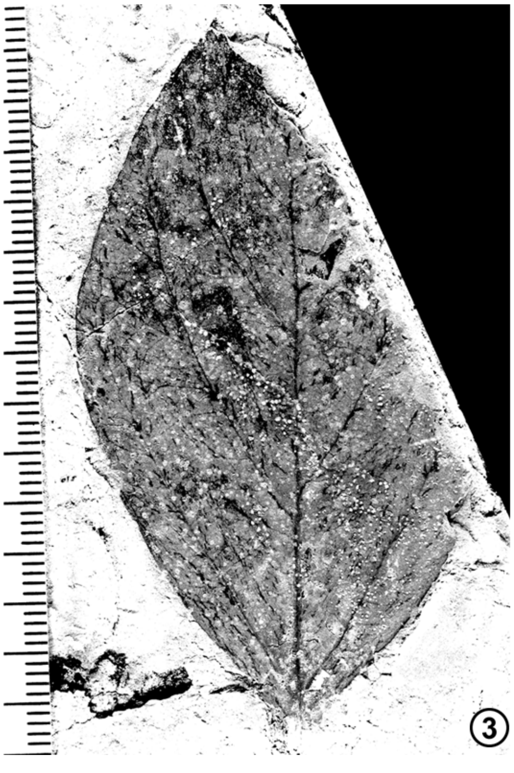

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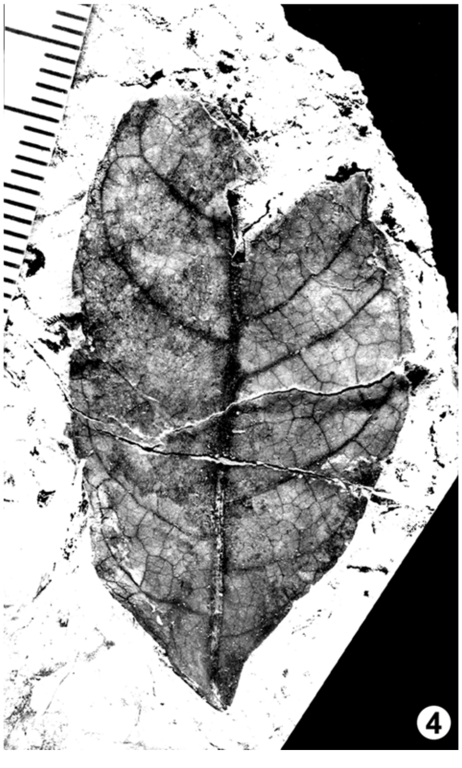
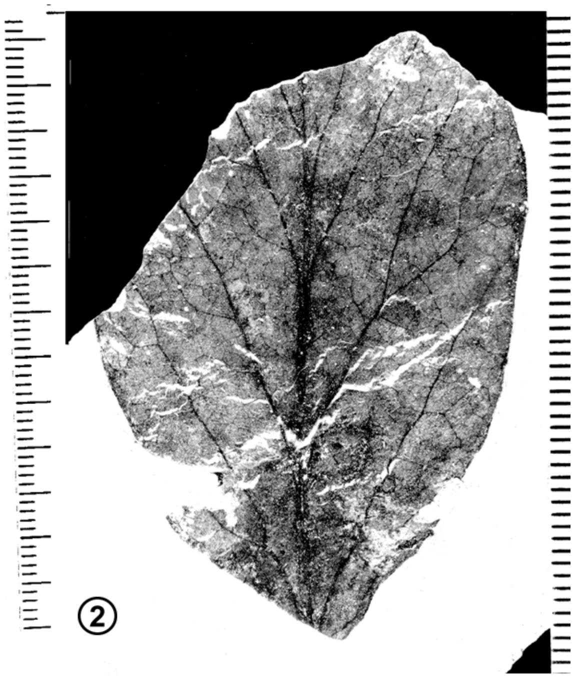


④

PLATE 36


①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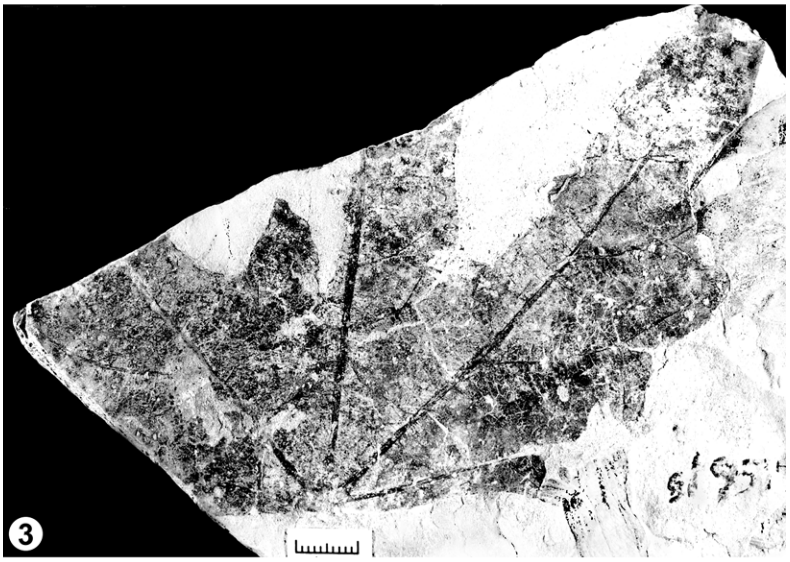
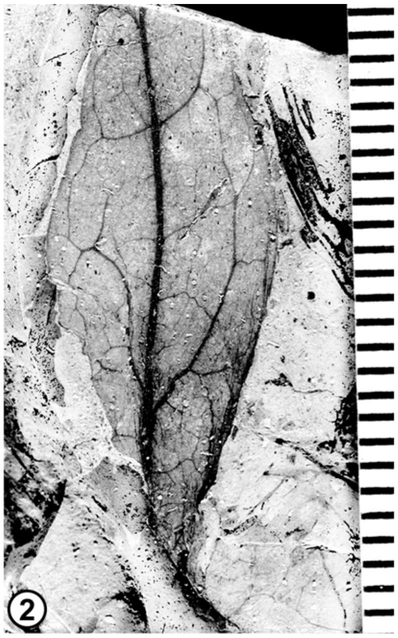

③


④

PLATE 37

①



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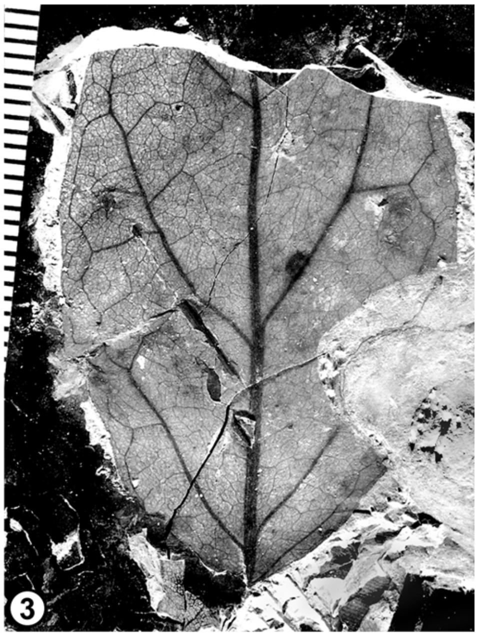
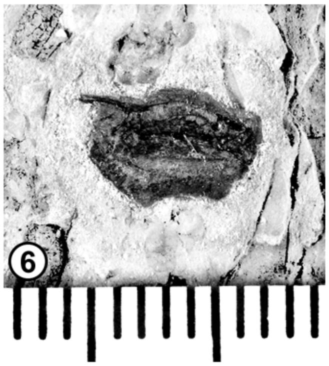


③

④

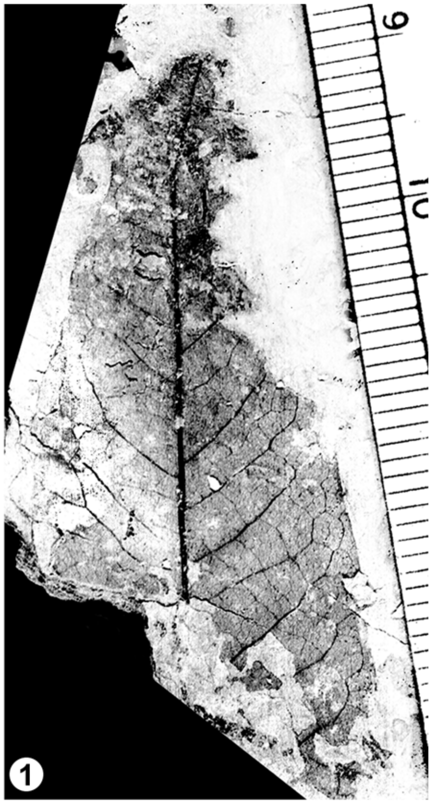
⑤



⑥

⑦

PLATE 38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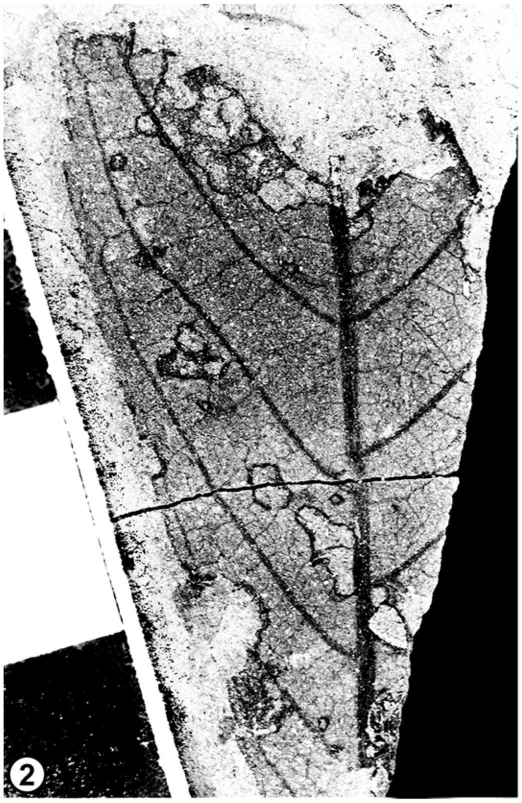
2

Appendix 6.1. Complete locality matrix for morphotypes (listed alphabetically by morphotype number). Sampling levels (see Table 5.1): 2 = lumped Clarkforkian; 3 = Big Multi local section; 4 = Main Body of Wasatch Fm.; 5 = Latham; 6 = Sourdough; 7 = Niland Tongue; 8 = Wilkins Peak. Only last three digits of USNM localities are shown, all prefixed by “41-“ (see Appendix 5.1). 1 = present at locality; 0 = absent at locality; sl = found within 1-20 m along strike (same level) but not at locality; nv = missing voucher. * = Wasatchian locality in Ramsey Ranch Member of Wasatch Formation, not in Great Divide Basin, not specifically correlatable either to the Latham or Sourdough sampling levels. “L” = locality in Luman Tongue of Green River Formation. “PW” = UCMP loc. PA 116, Little Mountain, Wilkins Peak Member of Green River Fm. “PL” = UCMP loc. PA 116, Laney Member of Green River Fm. USNM loc. 41427 is the same as UF locality 15882; USNM locality 41278 is the same as UF loc. 18126 and DMNH loc. 15270 (Appendix 5.1). “f” = raw frequency of morphotype at all localities, not including “sl” and “nv” occurrences (i.e., a row sum). The frequency of some morphotypes therefore appears as zero.

Morpho type	Sampling level / USNM locality no. 41-													
	2	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
	252	**254**	**255**	**256**	**257**	**258**	**259**	**260**	**261**	**277**	**278**	**279**	**280**	**281**
FW01	0	0	1	0	0	1	0	1	0	0	0	1	1	1
FW02	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW03	0	0	0	0	1	0	0	0	0	1	1	0	0	1
FW04	0	0	0	0	0	0	0	0	0	1	0	0	0	0
FW05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW06	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW08	0	1	0	0	1	1	0	0	1	1	0	1	0	0
FW09	0	0	0	0	0	0	0	0	0	0	0	0	0	sl
FW14	0	0	0	1	0	1	0	1	1	0	0	0	0	0
FW15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW16	0	0	0	0	0	0	0	0	0	0	0	0	0	1
FW18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW19	0	1	1	0	0	0	0	0	0	1	1	0	0	0
FW20	0	1	0	0	0	0	0	1	0	0	1	1	0	1
FW21	0	0	0	0	0	0	0	0	0	1	0	0	0	0
FW23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW25	0	0	0	0	0	0	0	0	0	1	0	1	0	0
FW26	0	0	0	0	0	0	0	0	0	0	0	0	0	sl
FW27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW28	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW30	0	0	0	0	0	0	0	0	0	0	0	0	0	1
FW31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW32	0	0	0	0	0	0	0	0	0	0	0	1	0	0
FW34	0	1	0	0	0	0	0	0	1	0	1	0	0	0
FW39	1	0	0	0	0	0	0	0	0	0	0	0	0	0
FW40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW43	0	0	0	0	0	1	0	0	1	0	1	0	0	0
FW44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW48	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW49	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW50	0	0	0	0	0	0	0	0	0	0	1	0	0	1
FW51	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW52	0	0	0	0	1	0	0	0	0	0	0	0	0	0
FW54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW57	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW58	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	Sampling level / USNM locality no. 41-													
	2	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
	252	**254**	**255**	**256**	**257**	**258**	**259**	**260**	**261**	**277**	**278**	**279**	**280**	**281**
FW59	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW60	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW61	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW62	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW63	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR501	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR502	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR503	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR504	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR505	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR506	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR507	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR508	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR509	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR511	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR512	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR513	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR515	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR516	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR517	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR518	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR520	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR521	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR522	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR523	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR524	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR525	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR526	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR528	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR529	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR530	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR531	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR532	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR533	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR534	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR535	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR536	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	Sampling level / USNM locality no. 41-													
	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	252	254	255	256	257	258	259	260	261	277	278	279	280	281
GR538	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR539	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR542	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR543	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR545	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR546	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR547	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR549	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR550	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR551	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR552	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR553	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR554	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR555	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR556	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR03	0	0	0	0	1	0	0	0	0	0	0	0	0	0
RR04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR06	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR07a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR19	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR26	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	Sampling level / USNM locality no. 41-													
	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	252	254	255	256	257	258	259	260	261	277	278	279	280	281
RR27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR32	0	1	0	0	1	0	0	0	0	0	0	0	0	0
RR34	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR35	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR36	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR37	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR38	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR41	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR42	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR46	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR47	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR53	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR56	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR57	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR64	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR69	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR70	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR71	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR72	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	2	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
	252	**254**	**255**	**256**	**257**	**258**	**259**	**260**	**261**	**277**	**278**	**279**	**280**	**281**
RR73	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR74	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR78	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR79	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR82	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR83	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR84	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR85	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR86	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR87	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR89	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	**1**	**5**	**2**	**1**	**5**	**4**	**0**	**3**	**4**	**6**	**17**	**5**	**1**	**6**

Morph otype	Sampling level / USNM locality no. 41-													
	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	282	283	284	285	286	287	288	289	290	291	292	293	294	295
FW01	1	1	1	0	1	0	1	1	0	1	0	1	0	1
FW02	0	0	0	0	1	0	0	0	1	1	0	0	0	1
FW03	0	0	0	0	1	1	0	1	0	1	1	1	0	0
FW04	1	0	1	1	1	0	0	0	0	1	0	1	1	0
FW05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW06	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW08	0	0	0	0	0	1	1	1	1	0	1	0	1	1
FW09	1	0	0	0	0	0	0	0	0	0	0	0	0	0
FW14	0	0	0	0	0	1	0	0	1	0	0	0	0	1
FW15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW16	1	0	1	0	1	0	0	1	0	0	0	1	0	0
FW18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW19	0	0	0	0	0	0	0	0	0	0	0	0	0	1
FW20	1	1	1	0	0	0	0	0	1	1	0	1	1	0
FW21	0	0	0	1	0	0	0	1	0	0	0	0	0	1
FW23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW28	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW29	0	0	0	0	0	0	0	0	0	0	0	0	0	1
FW30	1	0	0	0	0	0	0	1	0	0	0	0	0	nv
FW31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW34	0	0	0	0	0	1	0	0	0	0	1	0	0	0
FW39	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW43	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW44	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW45	0	0	0	0	0	0	0	0	0	0	1	0	0	0
FW48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW57	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morphotype	Sampling level / USNM locality no. 41-													
	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	282	283	284	285	286	287	288	289	290	291	292	293	294	295
FW58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW61	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW66	0	0	0	1	0	0	0	0	0	0	0	0	0	0
FW67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR501	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR502	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR503	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR504	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR505	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR506	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR507	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR508	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR509	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR511	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR512	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR513	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR515	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR516	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR517	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR518	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR520	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR521	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR522	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR523	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR524	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR525	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR526	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR528	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR529	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR530	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR531	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR532	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR533	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR534	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR535	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morphotype	Sampling level / USNM locality no. 41-													
	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	282	283	284	285	286	287	288	289	290	291	292	293	294	295
GR536	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR538	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR539	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR542	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR543	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR545	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR546	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR547	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR549	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR550	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR551	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR552	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR553	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR554	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR555	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR556	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR03	0	0	0	0	0	0	0	0	0	0	0	0	0	1
RR04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR06	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR07a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR19	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR24	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morphotype	Sampling level / USNM locality no. 41-													
	2	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
	282	**283**	**284**	**285**	**286**	**287**	**288**	**289**	**290**	**291**	**292**	**293**	**294**	**295**
RR26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR32	0	0	0	0	0	0	0	1	0	0	1	0	1	0
RR34	0	0	0	0	0	0	0	0	0	0	1	0	0	0
RR35	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR36	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR37	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR38	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR41	0	0	0	1	0	0	0	0	0	0	0	0	1	0
RR42	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR46	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR47	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR53	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR56	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR57	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR64	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR69	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR70	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR71	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morphotype	Sampling level / USNM locality no. 41-													
	2	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**
	282	**283**	**284**	**285**	**286**	**287**	**288**	**289**	**290**	**291**	**292**	**293**	**294**	**295**
RR72	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR73	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR74	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR78	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR79	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR82	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR83	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR84	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR85	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR86	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR87	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR89	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	**6**	**2**	**4**	**4**	**5**	**4**	**2**	**7**	**4**	**5**	**8**	**5**	**5**	**8**

Morpho type	Sampling level / USNM locality no. 41-													
	2	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
	296	**297**	**298**	**299**	**300**	**301**	**262**	**263**	**264**	**265**	**266**	**267**	**268**	**269**
FW01	1	1	1	0	1	1	1	1	0	1	1	1	1	1
FW02	0	1	0	0	0	0	1	1	0	0	0	0	0	0
FW03	1	0	0	0	1	0	0	0	0	0	0	1	1	0
FW04	0	0	0	0	0	0	0	0	0	1	0	0	0	0
FW05	0	0	0	0	0	0	0	0	0	0	0	0	0	1
FW06	0	0	0	0	0	0	0	0	0	0	0	0	0	1
FW07	1	0	0	0	1	0	0	0	0	0	0	1	0	0
FW08	0	1	1	1	1	1	1	1	0	0	1	1	0	0
FW09	0	0	0	0	1	0	1	1	0	0	0	1	0	1
FW14	1	0	1	0	1	0	0	0	0	1	1	1	1	0
FW15	0	0	0	0	0	0	0	0	0	1	0	0	0	0
FW16	1	0	0	0	0	0	1	1	0	1	0	1	1	1
FW18	0	0	0	0	0	0	0	0	0	0	0	1	0	0
FW19	1	0	0	0	0	0	0	0	0	0	0	0	1	0
FW20	1	0	0	0	1	0	1	1	1	1	0	1	1	1
FW21	0	1	1	0	0	1	0	0	0	0	0	0	0	0
FW23	0	0	0	0	0	0	0	0	0	0	0	0	0	1
FW24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW25	1	0	0	0	0	0	0	0	0	1	0	0	0	0
FW26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW27	1	0	0	0	1	0	0	1	0	0	0	0	0	0
FW28	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW30	1	0	0	0	1	0	0	0	0	0	0	0	0	0
FW31	0	0	0	0	0	0	0	0	0	0	0	0	1	0
FW32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW34	0	0	0	0	0	0	0	1	0	0	0	0	0	0
FW39	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW54	0	0	0	0	0	0	1	0	0	0	0	0	0	0
FW55	1	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	2	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
	296	**297**	**298**	**299**	**300**	**301**	**262**	**263**	**264**	**265**	**266**	**267**	**268**	**269**
FW57	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW61	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW65	0	0	0	0	0	0	0	0	1	0	0	0	0	0
FW66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW67	1	0	0	0	0	0	0	0	0	0	0	0	0	0
FW68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR501	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR502	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR503	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR504	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR505	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR506	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR507	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR508	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR509	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR511	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR512	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR513	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR515	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR516	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR517	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR518	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR520	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR521	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR522	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR523	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR524	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR525	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR526	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR528	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR529	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR530	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR531	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR532	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR533	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	Sampling level / USNM locality no. 41-													
	2	2	2	2	2	2	3	3	3	3	3	3	3	3
	296	297	298	299	300	301	262	263	264	265	266	267	268	269
GR534	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR535	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR536	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR538	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR539	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR542	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR543	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR545	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR546	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR547	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR549	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR550	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR551	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR552	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR553	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR554	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR555	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR556	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR03	0	0	0	0	0	0	0	0	1	0	1	0	0	0
RR04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR06	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR07a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR19	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR21	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	Sampling level / USNM locality no. 41-													
	2	2	2	2	2	2	3	3	3	3	3	3	3	3
	296	297	298	299	300	301	262	263	264	265	266	267	268	269
RR22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR34	0	0	0	0	0	0	0	0	0	0	0	sl	0	0
RR35	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR36	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR37	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR38	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR41	0	0	0	1	1	1	0	0	1	sl	0	0	0	0
RR42	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR46	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR47	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR53	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR56	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR57	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR64	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR67	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	2	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**
	296	**297**	**298**	**299**	**300**	**301**	**262**	**263**	**264**	**265**	**266**	**267**	**268**	**269**
RR68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR69	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR70	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR71	0	0	0	0	0	0	0	0	1	0	0	0	0	0
RR72	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR73	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR74	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR78	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR79	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR82	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR83	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR84	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR85	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR86	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR87	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR89	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	**12**	**4**	**4**	**2**	**10**	**4**	**7**	**8**	**5**	**7**	**4**	**9**	**7**	**7**

Morpho type	Sampling level / USNM locality no. 41-													
	3	**3**	**3**	**3**	**3**	**3**	**3**	**4**	**4**	**4**	**4**	**4**	**4**	*****
	270	**271**	**272**	**273**	**274**	**275**	**276**	**306**	**307**	**308**	**309**	**310**	**311**	**323**
FW01	1	0	1	1	1	0	0	1	0	0	0	1	0	0
FW02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW03	1	0	1	1	1	0	0	0	0	0	0	0	0	0
FW04	0	0	0	0	0	0	0	0	1	0	1	0	0	0
FW05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW06	1	0	0	0	1	0	0	0	0	0	0	0	0	0
FW07	1	0	0	0	1	0	0	0	0	0	0	0	0	0
FW08	1	1	1	0	1	1	1	0	0	0	0	0	0	0
FW09	0	0	1	sl	1	0	0	0	0	0	0	0	0	0
FW14	1	1	0	1	1	0	0	0	0	0	0	0	0	0
FW15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW16	1	0	0	0	1	0	0	0	0	0	0	0	0	0
FW18	0	0	1	0	0	0	0	0	0	0	0	0	0	0
FW19	1	0	1	0	0	0	0	0	0	0	0	0	0	0
FW20	1	1	1	1	1	0	0	0	0	0	0	0	0	0
FW21	0	0	0	0	1	0	0	0	0	0	1	0	0	0
FW23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW24	0	0	0	0	1	0	0	0	0	0	0	0	0	0
FW25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW28	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW29	0	0	0	0	0	0	0	0	1	0	0	0	0	0
FW30	1	0	0	0	0	0	0	0	0	0	1	0	0	0
FW31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW34	1	0	1	0	1	0	0	0	0	0	0	0	0	0
FW39	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW40	1	0	0	0	1	0	0	0	0	0	0	0	0	0
FW43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW55	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	Sampling level / USNM locality no. 41-													
	3	**3**	**3**	**3**	**3**	**3**	**3**	**4**	**4**	**4**	**4**	**4**	**4**	*****
	270	**271**	**272**	**273**	**274**	**275**	**276**	**306**	**307**	**308**	**309**	**310**	**311**	**323**
FW57	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW58	1	0	0	0	0	0	0	0	0	0	0	0	0	0
FW59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW61	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW66	1	0	0	0	0	0	0	0	0	0	0	0	0	0
FW67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW68	0	0	0	0	1	0	0	0	0	0	0	0	0	0
GR501	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR502	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR503	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR504	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR505	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR506	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR507	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR508	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR509	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR511	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR512	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR513	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR515	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR516	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR517	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR518	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR520	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR521	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR522	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR523	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR524	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR525	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR526	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR528	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR529	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR530	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR531	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR532	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR533	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	3	**3**	**3**	**3**	**3**	**3**	**3**	**4**	**4**	**4**	**4**	**4**	**4**	*****
	270	**271**	**272**	**273**	**274**	**275**	**276**	**306**	**307**	**308**	**309**	**310**	**311**	**323**
GR534	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR535	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR536	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR538	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR539	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR542	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR543	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR545	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR546	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR547	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR549	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR550	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR551	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR552	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR553	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR554	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR555	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR556	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR01	0	0	0	0	0	0	0	0	0	0	0	0	0	1
RR02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR03	0	0	0	0	0	0	0	0	0	0	0	0	1	0
RR04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR06	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR07a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR19	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR21	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	3	**3**	**3**	**3**	**3**	**3**	**3**	**4**	**4**	**4**	**4**	**4**	**4**	*****
	270	**271**	**272**	**273**	**274**	**275**	**276**	**306**	**307**	**308**	**309**	**310**	**311**	**323**
RR22	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR32	0	1	1	1	1	0	0	0	1	0	1	0	0	0
RR34	0	0	1	0	0	0	0	0	0	0	0	0	0	0
RR35	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR36	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR37	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR38	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR41	1	0	1	0	0	0	0	0	0	0	0	0	1	0
RR42	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR46	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR47	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR53	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR56	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR57	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR64	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR67	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	3	**3**	**3**	**3**	**3**	**3**	**3**	**4**	**4**	**4**	**4**	**4**	**4**	*****
	270	**271**	**272**	**273**	**274**	**275**	**276**	**306**	**307**	**308**	**309**	**310**	**311**	**323**
RR68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR69	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR70	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR71	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR72	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR73	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR74	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR78	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR79	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR82	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR83	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR84	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR85	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR86	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR87	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR89	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM04	0	0	0	0	0	0	0	0	1	0	0	0	0	0
WM16	0	0	0	0	0	0	0	1	0	1	0	0	0	0
WM21	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Total	**15**	**4**	**11**	**5**	**15**	**1**	**1**	**3**	**4**	**1**	**4**	**1**	**2**	**1**

Morpho type	**Sampling level / USNM locality no. 41-**													
	*****	*****	*****	*****	*****	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**6**	**6**
	324	**325**	**326**	**327**	**328**	**316**	**317**	**318**	**319**	**320**	**321**	**322**	**329**	**330**
FW01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW03	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW06	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW08	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW19	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW28	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW30	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW34	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW39	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW55	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	*****	*****	*****	*****	*****	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**6**	**6**
	324	**325**	**326**	**327**	**328**	**316**	**317**	**318**	**319**	**320**	**321**	**322**	**329**	**330**
FW57	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW61	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR501	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR502	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR503	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR504	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR505	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR506	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR507	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR508	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR509	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR511	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR512	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR513	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR515	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR516	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR517	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR518	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR520	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR521	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR522	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR523	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR524	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR525	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR526	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR528	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR529	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR530	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR531	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR532	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR533	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	*****	*****	*****	*****	*****	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**6**	**6**
	324	**325**	**326**	**327**	**328**	**316**	**317**	**318**	**319**	**320**	**321**	**322**	**329**	**330**
GR534	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR535	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR536	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR538	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR539	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR542	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR543	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR545	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR546	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR547	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR549	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR550	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR551	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR552	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR553	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR554	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR555	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR556	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR01	1	1	1	0	1	1	1	1	0	0	sl	0	0	0
RR02	0	0	0	0	1	0	0	0	0	0	0	0	1	1
RR03	0	1	1	0	1	0	1	0	0	0	1	0	sl	1
RR04	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR05	0	0	0	0	1	0	0	0	0	1	sl	0	1	1
RR06	0	0	0	0	0	0	1	0	0	0	1	0	0	1
RR07	0	0	0	0	0	0	1	0	0	0	1	0	0	0
RR07a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR11	0	0	0	0	0	0	0	0	0	1	0	0	0	0
RR12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14	0	0	0	0	0	0	1	0	0	0	0	1	0	0
RR14a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR17	0	0	0	0	0	0	0	0	0	0	sl	0	1	0
RR18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR19	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR21	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	*****	*****	*****	*****	*****	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**6**	**6**
	324	**325**	**326**	**327**	**328**	**316**	**317**	**318**	**319**	**320**	**321**	**322**	**329**	**330**
RR22	0	0	0	0	0	1	1	1	1	0	0	0	0	0
RR23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR34	0	0	0	0	0	0	1	0	0	0	0	0	0	0
RR35	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR36	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR37	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR38	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR41	0	0	0	0	0	0	0	0	0	0	1	0	1	0
RR42	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR46	0	0	0	0	0	0	1	0	0	0	sl	0	0	0
RR47	0	0	0	0	0	0	1	0	0	0	0	0	0	0
RR48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR52	0	0	0	0	0	0	1	0	0	1	sl	1	0	0
RR53	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR54	0	0	0	0	0	0	0	sl	1	0	sl	0	0	0
RR55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR56	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR57	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR64	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR67	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	*****	*****	*****	*****	*****	**5**	**5**	**5**	**5**	**5**	**5**	**5**	**6**	**6**
	324	**325**	**326**	**327**	**328**	**316**	**317**	**318**	**319**	**320**	**321**	**322**	**329**	**330**
RR68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR69	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR70	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR71	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR72	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR73	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR74	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR78	0	0	0	0	0	1	1	0	1	1	0	1	0	0
RR79	0	0	0	0	0	0	1	0	0	0	0	0	0	0
RR80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR82	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR83	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR84	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR85	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR86	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR87	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR89	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	**1**	**2**	**2**	**0**	**4**	**3**	**12**	**2**	**3**	**4**	**4**	**5**	**4**	**4**

Morpho type	**Sampling level / USNM locality no. 41-**													
	6	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**
	331	**332**	**333**	**334**	**335**	**336**	**337**	**338**	**339**	**340**	**341**	**342**	**343**	**344**
FW01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW03	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW06	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW08	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW19	0	0	0	0	0	0	0	0	0	0	1	0	1	0
FW20	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW21	0	0	0	0	0	1	0	0	0	1	1	1	0	0
FW23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW28	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW30	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW34	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW39	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW57	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	6	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**
	331	**332**	**333**	**334**	**335**	**336**	**337**	**338**	**339**	**340**	**341**	**342**	**343**	**344**
FW58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW61	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR501	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR502	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR503	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR504	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR505	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR506	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR507	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR508	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR509	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR511	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR512	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR513	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR515	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR516	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR517	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR518	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR520	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR521	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR522	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR523	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR524	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR525	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR526	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR528	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR529	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR530	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR531	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR532	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR533	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR534	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR535	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	Sampling level / USNM locality no. 41-													
	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	331	332	333	334	335	336	337	338	339	340	341	342	343	344
GR536	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR538	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR539	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR542	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR543	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR545	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR546	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR547	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR549	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR550	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR551	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR552	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR553	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR554	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR555	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR556	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR01	0	0	0	1	0	1	0	0	0	1	1	1	1	1
RR02	1	1	1	1	0	0	0	0	0	0	0	1	0	0
RR03	0	0	0	0	0	1	1	1	0	0	1	1	1	0
RR04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR05	0	0	1	1	0	0	0	0	1	0	0	1	0	1
RR06	0	1	0	0	0	0	0	0	0	0	1	0	0	0
RR07	1	1	1	0	0	1	0	0	0	1	1	1	0	0
RR07a	0	1	0	0	0	nv	0	0	0	0	0	0	0	0
RR09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR10	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR12	1	0	0	0	0	0	0	1	1	0	1	1	0	0
RR13	0	0	0	0	0	0	0	0	1	0	0	0	0	0
RR14	0	1	0	0	1	1	0	1	1	0	0	1	0	0
RR14a	0	0	0	0	0	1	0	0	0	0	0	0	0	0
RR15	1	0	0	0	0	0	0	0	1	0	0	1	0	0
RR16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR17	0	0	0	0	0	0	0	0	1	0	0	1	0	0
RR18	0	0	0	0	0	0	0	0	0	0	1	1	0	0
RR19	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR20	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR21	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR22	0	sl	0	0	0	0	0	0	1	0	1	1	0	0
RR23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR24	0	0	0	0	0	0	0	0	0	0	0	1	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	6	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**
	331	**332**	**333**	**334**	**335**	**336**	**337**	**338**	**339**	**340**	**341**	**342**	**343**	**344**
RR26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR31	0	1	0	0	0	0	0	0	0	0	0	0	0	0
RR32	0	0	1	0	0	0	0	0	0	0	0	1	0	0
RR34	0	0	0	0	0	0	0	0	0	0	1	0	0	0
RR35	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR36	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR37	0	0	0	0	0	0	0	0	1	0	0	1	0	0
RR38	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR40	0	0	0	0	1	1	0	0	0	0	1	0	0	0
RR41	0	0	0	0	1	1	0	0	0	0	0	0	0	1
RR42	0	1	0	0	0	0	0	0	0	0	0	0	0	0
RR43	0	1	0	0	0	0	0	0	0	0	0	0	0	0
RR44	0	sl	0	0	0	1	0	0	1	0	0	0	0	0
RR45	0	0	0	0	0	0	0	0	0	1	0	0	0	0
RR46	0	0	0	0	0	sl	0	0	0	0	1	0	0	0
RR47	0	0	0	0	0	0	0	0	0	0	1	0	0	0
RR48	0	0	0	0	0	0	0	0	0	0	1	0	0	0
RR49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR50	0	0	0	0	0	0	0	0	0	0	1	0	0	0
RR51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR53	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR56	0	sl	0	0	0	0	0	0	0	0	0	0	0	0
RR57	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR58	0	0	0	0	0	0	1	0	0	0	0	0	0	0
RR59	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR60	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR62	0	1	0	0	0	0	0	0	0	0	1	0	0	0
RR63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR64	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR66	0	sl	0	0	0	0	0	0	0	0	0	0	0	0
RR67	0	0	0	0	0	0	0	0	0	0	1	0	0	0
RR68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR69	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR70	0	sl	0	0	0	0	0	0	0	0	0	0	0	0
RR71	0	sl	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	6	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**
	331	**332**	**333**	**334**	**335**	**336**	**337**	**338**	**339**	**340**	**341**	**342**	**343**	**344**
RR72	0	sl	0	0	0	0	0	0	0	0	0	0	0	0
RR73	0	sl	0	0	0	0	0	0	0	0	0	0	0	0
RR74	0	0	0	0	0	sl	0	0	0	0	0	0	0	0
RR75	0	0	0	0	0	1	0	0	0	0	0	0	0	0
RR78	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR79	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR82	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR83	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR84	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR85	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR86	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR87	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR89	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR90	0	0	0	0	0	0	0	0	0	0	0	1	0	0
RR91	0	0	0	0	0	0	0	0	0	0	sl	0	0	0
WM04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	**4**	**9**	**4**	**3**	**3**	**10**	**2**	**4**	**9**	**4**	**17**	**24**	**3**	**3**

Morpho type	Sampling level / USNM locality no. 41-													
	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	345	346	347	348	349	350	351	352	353	354	355	356	357	358
FW01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW03	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW06	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW07	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW08	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW14	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW15	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW18	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW19	0	0	0	0	1	0	1	1	sl	0	1	0	0	0
FW20	0	0	0	0	1	0	0	1	0	1	1	0	0	0
FW21	0	1	0	0	0	1	0	0	0	0	1	0	0	0
FW23	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW24	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW26	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW27	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW28	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW30	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW31	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW32	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW34	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW39	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW48	0	0	0	1	1	0	0	1	1	0	0	0	0	0
FW49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW57	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	Sampling level / USNM locality no. 41-													
	6	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**
	345	**346**	**347**	**348**	**349**	**350**	**351**	**352**	**353**	**354**	**355**	**356**	**357**	**358**
FW58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW59	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW61	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW63	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW65	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW66	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
FW68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR501	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR502	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR503	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR504	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR505	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR506	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR507	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR508	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR509	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR511	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR512	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR513	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR515	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR516	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR517	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR518	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR520	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR521	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR522	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR523	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR524	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR525	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR526	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR528	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR529	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR530	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR531	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR532	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR533	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR534	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR535	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	Sampling level / USNM locality no. 41-													
	6	6	6	6	6	6	6	6	6	6	6	6	6	6
	345	346	347	348	349	350	351	352	353	354	355	356	357	358
GR536	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR538	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR539	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR542	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR543	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR545	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR546	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR547	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR549	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR550	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR551	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR552	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR553	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR554	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR555	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GR556	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR01	1	1	0	0	0	1	0	0	0	1	0	1	1	1
RR02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR03	0	0	0	0	0	0	0	1	0	0	0	1	1	0
RR04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR05	1	0	0	1	1	0	0	1	1	0	0	0	0	1
RR06	0	0	0	0	0	0	0	0	0	0	0	0	1	0
RR07	1	1	0	0	0	1	0	1	0	0	0	1	1	0
RR07a	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR09	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR11	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR12	0	0	0	0	0	0	0	0	0	0	0	0	0	1
RR13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR14	0	0	1	1	1	1	1	1	0	1	1	0	0	1
RR14a	0	0	1	0	0	0	0	1	0	0	1	0	0	0
RR15	0	0	0	0	0	0	0	1	1	0	1	0	0	0
RR16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR17	0	0	0	0	0	0	0	1	sl	1	1	0	0	1
RR18	0	0	0	0	0	0	0	1	0	0	0	0	0	1
RR19	0	0	0	1	0	0	0	1	1	0	0	0	0	0
RR20	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR21	0	0	0	0	0	0	0	1	1	0	0	0	0	0
RR22	0	0	0	0	0	0	0	1	1	0	1	0	0	0
RR23	0	0	0	0	0	0	1	0	0	0	1	0	0	0
RR24	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	6	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**
	345	**346**	**347**	**348**	**349**	**350**	**351**	**352**	**353**	**354**	**355**	**356**	**357**	**358**
RR26	0	0	1	0	0	0	0	0	0	0	0	0	0	0
RR27	0	0	0	1	0	0	0	0	0	0	0	0	0	0
RR29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR31	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR32	0	0	1	0	0	0	1	0	1	0	0	0	0	1
RR34	0	0	0	0	0	0	0	0	1	0	0	0	0	0
RR35	0	0	0	1	0	0	0	1	1	0	0	0	0	0
RR36	0	0	0	0	0	0	0	1	1	0	0	0	0	0
RR37	0	0	0	0	0	0	0	1	1	0	0	0	0	1
RR38	0	0	0	0	0	0	0	0	1	0	0	0	0	0
RR40	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR41	1	1	0	0	0	0	0	0	0	0	0	0	0	0
RR42	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR43	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR44	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR45	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR46	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR47	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR48	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR49	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR51	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR52	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR53	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR54	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR55	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR56	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR57	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR58	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR59	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR60	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR62	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR63	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR64	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR65	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR66	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR67	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR68	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR69	0	0	0	0	0	0	1	0	sl	0	1	0	0	0
RR70	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR71	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Morpho type	**Sampling level / USNM locality no. 41-**													
	6	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**	**6**
	345	**346**	**347**	**348**	**349**	**350**	**351**	**352**	**353**	**354**	**355**	**356**	**357**	**358**
RR72	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR73	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR74	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR75	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR78	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR79	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR80	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR82	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR83	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR84	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR85	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR86	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR87	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR89	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RR90	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RR91	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM04	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM16	0	0	0	0	0	0	0	0	0	0	0	0	0	0
WM21	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	**4**	**4**	**4**	**6**	**5**	**4**	**5**	**26**	**12**	**4**	**10**	**3**	**4**	**8**

Morphotype	**Sampling level / USNM locality no. 41-**												
	6	**7**	**7**	**7**	**7**	**7**	**L**	**8**	**8**	**8**	**8**	**8**	***f***
	359	**360**	**361**	**362**	**363**	**364**	**367**	**368**	**370**	**427**	**PW**	**PL**	
FW01	0	0	0	0	0	0	0	0	0	0	0	0	33
FW02	0	0	0	0	0	0	0	0	0	0	0	0	8
FW03	0	0	0	0	0	0	0	0	0	0	0	0	18
FW04	0	0	0	0	0	0	0	0	0	0	0	0	11
FW05	0	0	0	0	0	0	0	0	0	0	0	0	1
FW06	0	0	0	0	0	0	0	0	0	0	0	0	3
FW07	0	0	0	0	0	0	0	0	0	0	0	0	5
FW08	0	0	0	0	0	0	0	0	0	0	0	0	28
FW09	0	0	0	0	0	0	0	0	0	0	0	0	8
FW14	0	0	0	0	0	0	0	0	0	0	0	0	18
FW15	0	0	0	0	0	0	0	0	0	0	0	0	1
FW16	0	0	0	0	0	0	0	0	0	0	0	0	15
FW18	0	0	0	0	0	0	0	0	0	0	0	0	2
FW19	1	0	0	0	0	0	0	0	0	0	0	0	16
FW20	0	0	0	0	0	0	0	0	0	1	0	1	32
FW21	0	0	0	0	0	0	0	1	0	0	0	0	16
FW23	0	0	0	0	0	0	0	0	0	0	0	0	1
FW24	0	0	0	0	0	0	0	0	0	0	0	0	1
FW25	0	0	0	0	0	0	0	0	0	0	0	0	4
FW26	0	0	0	0	0	0	0	0	0	0	0	0	0
FW27	0	0	0	0	0	0	0	0	0	0	0	0	3
FW28	0	0	0	0	0	0	0	0	0	0	0	0	1
FW29	0	0	0	0	0	0	0	0	0	0	0	0	2
FW30	0	0	0	0	0	0	0	0	0	0	0	0	7
FW31	0	0	0	0	0	0	0	0	0	0	0	0	1
FW32	0	0	0	0	0	0	0	0	0	0	0	0	1
FW34	0	0	0	0	0	0	0	0	0	0	0	0	9
FW39	0	0	0	0	0	0	0	0	0	0	0	0	1
FW40	0	0	0	0	0	0	0	0	0	0	0	0	2
FW43	0	0	0	0	0	0	0	0	0	0	0	0	4
FW44	0	0	0	0	0	0	0	0	0	0	0	0	1
FW45	0	0	0	0	0	0	0	0	0	0	0	0	1
FW48	0	0	0	0	0	0	0	0	0	0	0	0	5
FW49	0	0	0	0	0	0	0	0	0	0	0	0	1
FW50	0	0	0	0	0	0	0	0	0	0	0	0	2
FW51	0	0	0	0	0	0	0	0	0	0	0	0	1
FW52	0	0	0	0	0	0	0	0	0	0	0	0	1
FW54	0	0	0	0	0	0	0	0	0	0	0	0	1
FW55	0	0	0	0	0	0	0	0	0	0	0	0	1

Morphotype	Sampling level / USNM locality no. 41-											
	6	**7**	**7**	**7**	**7**	**7**	**L**	**8**	**8**	**8**	**8**	**8**	***f***
	359	**360**	**361**	**362**	**363**	**364**	**367**	**368**	**370**	**427**	**PW**	**PL**	
FW57	0	0	0	0	0	0	0	0	0	0	0	0	1
FW58	0	0	0	0	0	0	0	0	0	0	0	0	1
FW59	0	0	0	0	0	0	0	0	0	0	0	0	1
FW60	0	0	0	0	0	0	0	0	0	0	0	0	1
FW61	0	0	0	0	0	0	0	0	0	0	0	0	1
FW62	0	0	0	0	0	0	0	0	0	0	0	0	1
FW63	0	0	0	0	0	0	0	0	0	0	0	0	1
FW65	0	0	0	0	0	0	0	0	0	0	0	0	1
FW66	0	0	0	0	0	0	0	0	0	0	0	0	2
FW67	0	0	0	0	0	0	0	0	0	0	0	0	1
FW68	0	0	0	0	0	0	0	0	0	0	0	0	1
GR501	0	0	0	0	0	0	0	0	0	1	0	0	1
GR502	0	0	0	0	0	0	0	0	0	1	0	0	1
GR503	0	0	0	0	0	0	0	0	1	1	1	0	3
GR504	0	0	0	0	0	0	0	0	0	1	0	0	1
GR505	0	0	0	0	0	0	0	0	0	1	0	0	1
GR506	0	0	0	0	0	0	0	0	0	1	0	0	1
GR507	0	0	0	0	0	0	0	0	0	1	0	0	1
GR508	0	0	0	0	0	0	0	1	0	1	0	1	3
GR509	0	0	0	0	0	0	0	0	0	1	0	0	1
GR511	0	0	0	0	0	0	0	0	1	1	1	0	3
GR512	0	0	0	0	0	0	0	0	1	1	1	0	3
GR513	0	0	0	0	0	0	0	0	0	1	0	0	1
GR515	0	0	0	0	0	0	0	0	1	1	1	0	3
GR516	0	0	0	0	0	0	0	0	0	1	0	0	1
GR517	0	0	0	0	0	0	0	0	1	1	1	0	3
GR518	0	0	0	0	0	0	0	0	0	1	1	0	2
GR520	0	0	0	0	0	0	0	0	1	1	1	1	4
GR521	0	0	0	0	0	0	0	0	1	1	1	1	4
GR522	0	0	0	0	0	0	0	0	0	1	0	0	1
GR523	0	0	0	0	0	0	0	0	0	1	0	0	1
GR524	0	0	0	0	0	0	0	0	1	0	0	0	1
GR525	0	0	0	0	0	0	0	0	1	1	1	0	3
GR526	0	0	0	0	0	0	0	0	1	0	0	0	1
GR528	0	0	0	0	0	0	0	0	1	1	0	0	2
GR529	0	0	0	0	0	0	0	0	1	1	1	0	3
GR530	0	0	0	0	0	0	0	0	0	0	1	0	1
GR531	0	0	0	0	0	0	0	0	0	1	1	1	3
GR532	0	0	0	0	0	0	0	0	0	1	0	1	2
GR533	0	0	0	0	0	0	0	0	0	1	0	0	1

Morphotype	**Sampling level / USNM locality no. 41-**												
	6	**7**	**7**	**7**	**7**	**7**	**L**	**8**	**8**	**8**	**8**	**8**	***f***
	359	**360**	**361**	**362**	**363**	**364**	**367**	**368**	**370**	**427**	**PW**	**PL**	
GR534	0	0	0	0	0	0	0	0	0	1	0	0	1
GR535	0	0	0	0	0	0	0	0	0	1	0	1	2
GR536	0	0	0	0	0	0	0	0	1	0	0	0	1
GR538	0	0	0	0	0	0	0	0	1	0	0	0	1
GR539	0	0	0	0	0	0	0	0	0	0	1	0	1
GR542	0	0	0	0	0	0	0	0	0	1	0	0	1
GR543	0	0	0	0	0	0	0	0	0	0	0	1	1
GR545	0	0	0	0	0	0	0	0	0	0	1	0	1
GR546	0	0	0	0	0	0	0	0	0	0	1	0	1
GR547	0	0	0	0	0	0	0	0	1	1	1	1	4
GR549	0	0	0	0	0	0	0	0	0	1	0	0	1
GR550	0	0	0	0	0	0	0	0	0	1	0	0	1
GR551	0	0	0	0	0	0	0	0	0	1	0	0	1
GR552	0	0	0	0	0	0	0	0	0	1	0	0	1
GR553	0	0	0	0	0	0	0	0	0	1	0	0	1
GR554	0	0	0	0	0	0	0	0	0	1	0	0	1
GR555	0	0	0	0	0	0	0	0	1	0	0	0	1
GR556	0	0	0	0	0	0	0	0	0	1	0	0	0
RR01	0	0	0	0	0	0	0	0	0	0	0	0	22
RR02	0	0	0	0	0	0	0	0	0	0	0	0	8
RR03	1	1	0	1	1	1	0	0	0	0	0	0	25
RR04	0	0	0	0	0	0	0	0	0	0	0	0	1
RR05	1	0	1	0	0	0	0	0	0	0	0	0	17
RR06	0	0	1	1	0	0	0	0	0	0	0	0	8
RR07	0	0	0	1	0	0	0	0	0	0	0	0	16
RR07a	0	0	0	0	0	0	0	0	0	0	0	0	1
RR09	0	1	1	1	0	1	0	0	0	0	0	0	4
RR10	0	0	0	0	0	0	0	0	0	0	0	0	1
RR11	0	0	0	0	0	0	0	0	0	0	0	0	1
RR12	0	0	0	0	0	0	0	0	0	0	0	0	6
RR13	1	0	0	0	0	0	0	0	0	0	0	0	2
RR14	0	0	0	1	0	0	0	0	0	1	0	0	19
RR14a	1	0	0	0	0	0	0	0	0	0	0	0	5
RR15	0	0	0	0	0	0	0	0	0	0	0	0	6
RR16	0	0	1	0	0	0	0	0	0	0	0	0	1
RR17	1	0	0	0	0	0	0	0	0	0	0	0	8
RR18	1	0	0	0	0	0	0	0	0	0	0	0	5
RR19	0	0	0	0	0	0	0	0	0	0	0	0	4
RR20	0	0	0	0	0	0	0	0	0	0	0	0	2
RR21	0	0	0	0	0	0	0	0	0	0	0	0	3

Morphotype	**Sampling level / USNM locality no. 41-**											
	6	**7**	**7**	**7**	**7**	**7**	**L**	**8**	**8**	**8**	**8**	**8**	***f***
	359	**360**	**361**	**362**	**363**	**364**	**367**	**368**	**370**	**427**	**PW**	**PL**	
RR22	0	0	0	0	0	0	0	0	0	0	0	0	10
RR23	0	0	0	0	0	0	0	0	0	0	1	0	3
RR24	0	0	0	0	0	0	0	0	0	0	0	0	1
RR26	0	0	0	0	0	0	0	0	0	0	0	0	1
RR27	0	0	0	0	0	0	0	0	0	0	0	0	1
RR29	0	0	0	1	0	0	0	0	0	0	0	0	1
RR31	0	0	0	0	0	0	0	0	0	0	0	0	2
RR32	1	0	0	0	0	0	0	0	0	0	0	0	18
RR34	0	0	0	1	0	0	0	1	1	0	0	0	7
RR35	0	0	0	0	0	0	0	0	0	0	0	0	3
RR36	0	0	0	0	0	0	0	0	0	0	0	0	3
RR37	0	0	0	0	0	0	0	0	0	0	0	0	5
RR38	0	0	0	0	0	0	0	0	0	0	0	0	1
RR40	0	0	0	0	0	0	0	0	0	0	0	0	3
RR41	0	0	0	1	0	0	0	0	1	1	0	0	19
RR42	0	0	0	0	0	0	0	0	0	0	0	0	1
RR43	0	0	0	0	0	0	0	0	0	0	0	0	1
RR44	0	0	1	0	0	0	0	0	0	0	0	0	3
RR45	0	0	0	0	0	0	0	0	0	0	0	0	1
RR46	0	0	0	0	0	0	0	0	0	0	0	0	2
RR47	0	0	0	0	0	0	0	0	0	0	0	0	2
RR48	0	0	0	0	0	0	0	0	0	0	0	0	1
RR49	0	0	0	1	0	0	0	0	0	0	0	0	1
RR50	0	0	0	0	0	0	0	0	0	0	0	0	1
RR51	0	0	0	1	0	0	0	0	0	0	0	0	1
RR52	0	0	0	0	0	0	0	0	0	0	0	0	3
RR53	0	0	0	0	0	0	0	0	0	0	0	0	1
RR54	0	0	0	0	0	0	0	0	0	0	0	0	1
RR55	0	0	0	1	0	0	0	0	0	0	0	0	1
RR56	0	0	0	0	0	0	0	0	0	0	0	0	0
RR57	0	0	0	0	0	0	0	0	0	0	0	0	1
RR58	0	0	0	0	0	0	0	0	0	0	0	0	1
RR59	0	0	0	0	0	0	0	0	0	0	0	0	2
RR60	0	0	1	1	0	0	0	0	0	0	0	0	3
RR62	0	0	1	0	0	0	0	0	0	0	0	0	4
RR63	0	0	0	0	0	0	0	0	0	0	0	0	1
RR64	0	0	0	0	0	0	0	0	0	0	0	0	1
RR65	0	0	0	0	0	0	0	0	0	0	0	0	1
RR66	0	0	0	0	0	0	0	0	0	0	0	0	1
RR67	0	0	0	0	0	0	0	0	0	0	0	0	1

Morphotype	**Sampling level / USNM locality no. 41-**												
	6	**7**	**7**	**7**	**7**	**7**	**L**	**8**	**8**	**8**	**8**	**8**	***f***
	359	**360**	**361**	**362**	**363**	**364**	**367**	**368**	**370**	**427**	**PW**	**PL**	
RR68	0	0	0	1	0	0	0	0	0	0	0	0	1
RR69	0	0	0	1	0	0	0	0	0	0	0	0	3
RR70	0	0	0	0	0	0	0	0	0	0	0	0	0
RR71	0	0	0	0	0	0	0	0	0	0	0	0	1
RR72	0	0	0	0	0	0	0	0	0	0	0	0	0
RR73	0	0	0	0	0	0	0	0	0	0	0	0	0
RR74	0	0	0	0	0	0	0	0	0	0	0	0	0
RR75	0	0	0	0	0	0	0	0	0	0	0	0	1
RR78	0	0	0	0	0	0	0	0	0	0	0	0	5
RR79	0	0	0	0	0	0	0	0	0	0	0	0	1
RR80	0	0	0	1	0	0	0	0	0	0	0	0	1
RR82	0	0	0	1	0	0	0	0	0	0	0	0	1
RR83	0	0	1	0	0	0	0	0	0	0	0	0	1
RR84	0	0	1	0	0	0	0	0	0	1	0	0	2
RR85	0	0	0	1	0	0	0	0	0	0	0	0	1
RR86	0	0	0	0	0	1	0	0	0	0	0	0	1
RR87	0	0	0	0	0	0	0	0	0	0	0	0	1
RR89	0	0	0	0	0	0	0	0	0	0	0	0	1
RR90	0	0	0	0	0	0	0	0	0	0	0	0	1
RR91	0	0	0	0	0	0	0	0	0	0	0	0	0
WM04	0	0	0	0	0	0	0	0	0	0	0	0	1
WM16	0	0	0	0	0	0	0	0	0	0	0	0	2
WM21	0	0	0	0	0	0	0	0	0	0	0	0	1
Total	**8**	**2**	**9**	**17**	**1**	**3**	**0**	**1**	**18**	**41**	**17**	**9**	

CHAPTER SEVEN

CONCLUSIONS

The major results of this investigation are summarized in the following numbered points:

(1) Leaf-margin analysis remains the most precise and effective method for estimating past mean annual temperatures from fossil leaf morphology.

(2) The number of species per sample has a major effect on the precision of leaf-margin analysis, both in predictor data sets and in fossil samples. This sampling error can be quantified, if sampling is random with respect to margin type, using a simple equation based on the standard deviation of binomially distributed outcomes.

(3) The effects of nonrandom sampling on leaf-margin analysis of fossil floras are best overcome by maximizing the number of species, the number of facies, and the transect length sampled per stratigraphic level. Predictor data sets for leaf-margin analysis should be collected over a sufficient area to minimize local biases caused by species abundance patterns and to maximize the number of species scored within a given climate.

(4) The relationship between leaf area and annual rainfall in living forests is highly significant and is revised here. Use of this revised correlation to estimate past mean annual precipitation is introduced as a new method, leaf-area analysis.

(5) Results from leaf-area analysis of seven Eocene floras from the Western U.S. indicate far wetter conditions than exist in the same areas today. Abundant moisture may have been an important factor in maintaining warm, frost-free conditions in the Eocene because of the major role of water vapor in retaining and transporting atmospheric heat.

(6) The Greater Green River Basin of southwestern Wyoming contains diverse and well-preserved paleofloras from the late Paleocene-early Eocene interval (Tiffanian, Clarkforkian, Wasatchian, and earliest Bridgerian North American Land Mammal Ages). These floras are ideal for investigations of climatic and biotic terrestrial events associated with Paleocene-Eocene global warming, which have previously been studied on a fine temporal scale only in the Bighorn Basin of northwestern Wyoming.

(7) Big Multi Quarry, in the Greater Green River Basin, is the most diverse fossil vertebrate locality yet known from the Clarkforkian Land Mammal Age. The quarry is closely associated stratigraphically with a well-exposed local section bearing nearly all of the species of fossil plants found from Clarkforkian rocks throughout the region. These organisms represent a floodplain ecosystem in a humid subtropical climate that existed before the latest Paleocene thermal maximum. Mean annual temperature was near 19.5°C and mean annual precipitation near 137 cm, with limited or no seasonal frost or marked dry season.

(8) The early Clarkforkian plant assemblage from the Big Multi local section more closely resembles middle than early Clarkforkian floras of the more northerly Bighorn Basin, suggesting northward floral migration in step with the overall Clarkforkian warming trend.

(9) Warm and wet conditions are associated in the early Eocene and today with moderately high plant species richness, mixed dominance, and spatial heterogeneity. However, plant communities found in the Clarkforkian Big Multi section were not species-rich, were strongly dominated by a single species, and were spatially homogeneous. These ecological conditions were typical of the cooler Tiffanian, despite the warm and humid Clarkforkian climate.

(10) Late Paleocene estimated mean annual temperature increased from about 13°C in the Tiffanian to nearly 20°C in the early Clarkforkian. Humid conditions prevailed, with annual rainfall near 150 cm. Mild climates continued in the Graybullian, although some cooling and drying may have taken place. Temperatures warmed again from the late Graybullian to the early Lostcabinian, and humid conditions returned. Early Lostcabinian mean annual temperatures were near 22°C and mean annual precipitation was again near 150 cm. Warm temperatures persisted in the later Lostcabinian and then dropped slightly in the earliest Bridgerian to about 19°C, as annual rainfall decreased sharply to approximately 75 cm in a more seasonal and arid climate. Generally frost-free conditions were present throughout the study interval, with the exception of the Tiffanian and possibly parts of the Graybullian.

(11) Eocene Lake Gosiute was not a primary cause of mild Eocene winters in southern Wyoming because the lake system was not present until the early Lostcabinian and not well developed until the middle Lostcabinian. Warm and equable conditions existed in the study area independent of possible lake effects.

(12) Vegetational response to Paleocene-Eocene climate changes was strongly pronounced. There were two turnover events that each involved the first and last appearances of over 80% of species. The first accompanied early Eocene warming, and the second coincided with drying in late early Eocene time. Major immigrations of families with modern tropical affinities occurred with Clarkforkian as well as early Eocene warming, although most families of plants known to be present in the late Paleocene persisted throughout the study interval. In similar depositional settings, early Eocene plant assemblages show greater diversity than either Tiffanian or Clarkforkian assemblages, in accord with the warmer early Eocene climate.

(13) These results from the Greater Green River Basin both complement and closely track the Bighorn Basin record at current levels of resolution. Similar climatic and biotic events have now been observed at all latitudes of Wyoming, showing that they are regional and not local in extent and increasing their value for understanding terrestrial events during the Paleocene-Eocene interval.

(14) Paleobotanical data are essential for understanding past climates. Climate research in “deep time” is highly relevant for understanding the effects of prolonged warming, cooling, wetting, and drying. These effects can only be modeled, not observed, in the present.