

**The Redmond fossil assemblage, a window into a Late
Cretaceous (Cenomanian) terrestrial ecosystem
in Eastern Canada**

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Contribution of Authors

Chapter 2, *Palaeoclimatic reconstruction for a Cenomanian-aged angiosperm flora near Schefferville, Labrador*, is a co-authored manuscript published at the journal *Palaeontology*. I am the first author on this article, with Hans Larsson as co-author. I visited the historic leaf collections from the Redmond no.1 mine and directed the collection of additional specimens during fieldwork in August 2018. I identified the leaf morphotypes and ran the CLAMP analysis to obtain climate parameter predictions. Additionally, I researched and wrote sections on the sampling uncertainties associated with CLAMP, the locality's depositional environment, its spatial and temporal resolution, and the North American context of these results.

Chapter 3, *First North American occurrence of hairy cicadas discovered in the Late Cretaceous (Cenomanian) Redmond Formation, Labrador, Canada*, is a co-authored manuscript in press at the journal *Acta Palaeontologica Polonica*. I am the first author on this manuscript, with Jacek Szwedo, an expert on hemipteran evolution, Cassia Paragnani and Hans Larsson as co-authors. I performed the examination of the fossil insect specimen that is the object of this paper, including vector drawings and photography with Reflectance Transformation Imaging. Ms Paragnani photographed wings of extant *Tettigarcta* specimens in the entomology collections of the National Museums Victoria, Melbourne, for comparison with the fossil specimen. I researched and wrote sections on the taxonomic relationships of this new species with extinct and extant relatives, and on the biogeography of this now relict family, with the precious assistance of Dr. Szwedo.

I prepared all other components of this thesis, including the general introduction, the literature review, the general discussion and the final conclusion.

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ABSTRACT

The Cenomanian-Turonian thermal maximum occurred in the middle of the Cretaceous Terrestrial Revolution, during which angiosperms began their diversification alongside many ecologically influential modern insect lineages. The extent of the influence of the physical environment and biotic interactions has yet to be properly determined for this major ecological and evolutionary transition, and the fundamental questions it raises can be addressed in part by constantly expanding the currently available fossil record.

This Master's thesis presents new research on the palaeoecology of the Redmond assemblage, a mysterious locality of estimated Cenomanian age from Labrador, near Schefferville, Canada. The fossils on which it is based consist in leaf and insect impressions, most of which have been discovered during the fieldwork associated with this project. The global environmental context of this unique fossil assemblage is presented in a literature review (Chapter 1) summarizing climate, vegetation and insect diversity trends in the middle of the Cretaceous.

The original research presented in this thesis is divided in two manuscripts: first, Chapter 2 presents a quantitative palaeoclimatic reconstruction for the Redmond locality based mostly on an examination of its angiosperm leaf flora. This analysis confirms previous predictions of a warm temperate to subtropical climate for the Quebec-Labrador Peninsula during this hothouse event. Along with this palaeoclimatological research, Chapter 3 delves into palaeoentomology with the presentation of the first hemipteran described from the Redmond assemblage. This new species constitutes a significant contribution to the entomofauna known from this site. The thesis is concluded with a discussion uniting the two manuscripts followed by prospects for future research on the Redmond assemblage (Chapter 4), a site that offers unique information on the environment of Eastern Canada during one of the most consequential biotic transitions in our planet's history.

RÉSUMÉ

Le pic thermique du Cénomanién-Turonien s'est déroulé au milieu de la Révolution terrestre du Crétacé, durant laquelle les angiospermes ont commencé leur diversification avec plusieurs lignées d'insectes modernes d'une grande importance écologique. Les étendues respectives de l'influence de l'environnement physique et des interactions biotiques restent à déterminer pour cette transition écologique et évolutive majeure et les questions fondamentales qu'elle soulève peuvent être abordées en partie par une expansion constante du registre fossile présentement disponible.

Ce mémoire de maîtrise présente de nouvelles recherches sur la paléoécologie de l'assemblage de Redmond, une mystérieuse localité d'âge (estimé) Cénomanién du Labrador, près de Schefferville, Canada. Les fossiles qui en sont le fondement consistent en des impressions de feuilles et d'insectes, la majorité ayant été découverte durant le travail de terrain associé à ce projet. Le contexte environnemental global de cette flore et faune uniques est présenté dans une revue de littérature (Chapitre 1) qui résume les tendances climatiques, de végétation et de diversité d'insectes au milieu du Crétacé.

La recherche originale présentée dans ce mémoire est divisée en deux manuscrits : premièrement, le Chapitre 2 présente une reconstruction paléoclimatique quantitative du site de Redmond basée surtout sur une examination de sa flore de feuilles d'angiospermes. Cette analyse confirme des prédictions précédentes d'un climat tempéré chaud à subtropical pour la péninsule du Québec-Labrador durant cette période de chaleur extrême. Aux côtés de cette recherche paléoclimatique, le Chapitre 3 s'immerge dans la paléoentomologie avec la présentation du premier hémiptère décrit de l'assemblage de Redmond. Cette nouvelle espèce constitue une contribution significative à l'entomofaune connue de ce site. Le mémoire est conclu par une discussion qui unit les deux manuscrits, suivie de pistes de recherche future sur l'assemblage de Redmond (Chapitre 4), un site qui offre de l'information unique sur l'environnement de l'Est du Canada durant une des transitions biotiques les plus conséquentes de l'histoire de notre planète.

CHAPTER 1. General introduction and literature review

1.1 General introduction

If evolution by natural selection was driven exclusively by biotic factors such as interspecific competition and arms races, as suggested by the Red Queen hypothesis (Van Valen 1973), origination and extinction rates would be relatively constant through time. These same rates would rise considerably during any catastrophic event or period of climate change, and remain almost null otherwise, if it was driven exclusively by extrinsic factors from the physical environment as proposed by Court Jester hypotheses (Barnosky 2001). However, an overview of the history of life shows that species originations and extinctions have happened all the time, whether at high rates during mass extinction events or lower rates during the normal ‘background’ condition (Jablonski 1986; Vos *et al.* 2015). Thus, the identification of the main drivers of species and community diversity remains one of the most fundamental questions in ecology and evolution. These two eco-evolutionary models have a profound influence on the investigation of universal biodiversity patterns, such as the causes of species turnover (Jablonski 1986), or latitudinal diversity gradients (Mittelbach *et al.* 2007).

Palaeontology contributes to this macroevolutionary debate, since the fossil record is the only direct source of information on the response of species and communities to disturbances on large spatial and temporal scales (Jablonski 1991, 2005). Investigations of the available fossil record currently support a multilevel mixed hypothesis according to which biotic factors drive community evolution locally and at short time scales, while changes in the physical environment have a stronger influence globally and in deep time (Gould 1985; Barnosky 2001; Benton 2009). In turn, these insights inform us on the long-term consequences of the present anthropogenic environmental changes that drive current species extinctions (Jablonski 1991). Considering the main challenges facing biodiversity today, past episodes of global warming (termed ‘hothouse events’) may be especially informative (Wing *et al.* 2005; Franks *et al.* 2014).

One of these events has a particularly high influence in eco-evolutionary theory because it occurred at the start of the Late Cretaceous period (the Cenomanian age), in the middle of a terrestrial ecosystem revolution characterized by a faunal and floral turnover that led to the diversification of flowering plants and of pollinating and eusocial insects (Crane *et al.* 1995; Grimaldi 1999; Grimaldi & Engel 2005). The Cretaceous Terrestrial Revolution constitutes an

interesting case study for testing the Red Queen and Court Jester hypotheses: there is ample evidence for plant-insect co-evolution driving origination and extinction in both of these ecologically influential clades, and the turnover reached its peak during the Cenomanian-Turonian thermal maximum (Grimaldi 1999; Labandeira 2014). In light of these considerations, was this biotic change caused predominantly by favourable climatic conditions, or rather by the multiplication of plant-insect associations leading to increasing specialization and speciation? Could it actually be caused by a combination of these factors?

Similar to the rest of the Phanerozoic, the fossil record for the middle of the Cretaceous contains large temporal and spatial gaps that create significant uncertainties on any biodiversity pattern detected for this time interval. For instance, the only Mesozoic site for the entire Quebec-Labrador Peninsula is the Redmond Formation, a very restricted sedimentary unit situated near Knob Lake and the iron mining town of Schefferville, Canada. It was brought to scientific attention by the discovery of plant and insect impression fossils, initially during trenching operations, and then during excursions led by Princeton University palaeobotanist Erling Dorf (1957) and the Geological Survey of Canada (1960, 1961) (Blais 1959; Dorf 1967; Rice 1969; Conliffe 2016). A Cenomanian age was proposed for this new fossil community by comparing its angiosperm flora with previously dated North American floras (Dorf 1959). No more fieldwork was conducted on the site for the following decades, during which the entire formation was destroyed by mining activities, until the Iron Ore Company of Canada ceased operations in 1982 (Clark 2011). As a result, it is now out of stratigraphical context.

In 2013, the Montreal-based *Musée de paléontologie et de l'évolution* (MPE) returned to the now abandoned Redmond no.1 mine. The aim of this four-day excursion was to collect from the float that was available at the surface of spoil piles surrounding the mine. This was followed by a month-long expedition in August 2018, led by the author of this thesis as a collaboration between the Redpath Museum and the MPE, which resulted in the largest single collection effort ever undertaken for the Redmond Formation.

This thesis aims to contribute to the integration of the Redmond ecosystem's expanded fossil record into our latest overview of the world during the Cretaceous Terrestrial Revolution. The first specific objective is to produce a precise and accurate estimate of the prevalent climatic conditions in this part of the world during the Cretaceous. The second specific objective is to

increase the biodiversity known from the site through the description of new plant and/or insect species.

The first chapter is a literature review of global Cretaceous climate, vegetation and insect diversity trends, with particular emphasis on the Albian-Cenomanian transition in the middle of this period. Since the Redmond Formation is most likely of Cenomanian age, its angiosperm-dominated flora probably existed in the middle of the Cretaceous Terrestrial Revolution that lay the foundations of modern terrestrial ecosystems. This review also assesses the advantages and limitations of the various palaeoclimate proxies that have been used to study this key period of Earth's history.

The second chapter presents an updated quantitative palaeoclimate reconstruction for Eastern Canada in the Cretaceous by applying the Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe 1993; Spicer 2006) to the Redmond Formation's angiosperm macroflora. Leaf physiognomy has long been known to predict a number of climate parameters, such as mean annual temperature and precipitation, while simultaneously providing information on community structure and composition (Bailey & Sinnott 1915; Wolfe 1979, 1993). The Redmond ecosystem's climate parameters will then be compared with the one previous quantitative estimate (Armstrong 1993), and with other Cretaceous North American localities to situate it in the Cenomanian's broad climatic trends (Wolfe & Upchurch 1987; Miller *et al.* 2006; Spicer & Herman 2010).

The third chapter consists in the first description to be completed among the new insect species discovered in the Redmond Formation over the 2013 and 2018 expeditions. It is the first 'hairy cicada' (family Tettigarctidae) known in the entire North American fossil record and is the first hemipteran described from this locality. This discovery is very significant for understanding the biogeography of a now relict insect family.

The fourth chapter is a general discussion that explores in greater detail the significance of the results outlined in the previous two chapters. It places the climate estimates for the Redmond Formation in a wider spatial and temporal context and further explores the place of its flora in the context of the angiosperm radiation, notably the appearance of the first large angiosperm trees. It also contains a summary and evaluation of alternative palaeoclimate proxies that could independently corroborate the signal from leaf physiognomy, with particular emphasis on the use of insects as environmental indicators. A final conclusion summarizes the research objectives that have been reached while suggesting further studies on the site's plant and insect diversity.

1.2 Environmental trends of terrestrial ecosystems in the middle of the Cretaceous

1.2.1 Introduction

The Cretaceous is the longest period of the Mesozoic era (~145.0 – ~66.0 Ma) (Cohen *et al.* 2018) and is defined by some of the most influential trends and events to have shaped the planet we know today. From a geological perspective, it is the period in which the final stages of the breakup of Pangaea occurred, when most of Earth's major landmasses reached their actual geographical position (Scotese 2001). From an eco-evolutionary perspective, it is the period in which the foundations of modern terrestrial ecosystems were established with the diversification of angiosperms (Crane & Lidgard 1989; Crane *et al.* 1995; Lupia *et al.* 2000) and of the vast majority of social and pollinating insect families (Grimaldi 1999; Ross *et al.* 2000; Grimaldi & Engel 2005; Labandeira 2014).

However, the Cretaceous world remained significantly different from today. From a climatological perspective, it was one of the 'greenhouse' periods of Earth's history, with fast ocean-floor spreading resulting in increased volcanic activity that led to CO₂ concentrations 8 – 10 times those of the Holocene (Barron & Washington 1985; Gale 2000; Franks *et al.* 2014; Hay *et al.* 2018). From an oceanographical perspective, this high tectonic activity led to a rise of ocean-basin margins that caused a general rise in eustatic sea levels, with epicontinental seas covering low-lying continental interiors (Gale 2000; Skelton 2003; Haq 2014). Indeed, both of the major Cretaceous sea-level highstands coincide with peaks in average seafloor spreading rate (Seton *et al.* 2009). The opening of major seaways increased poleward heat transport, which likely contributed to the lowering of pole-equator temperature gradients (Gale 2000; Hay 2008; Hay *et al.* 2018). In contrast to the polar location of deep-water formation in modern oceans, Cretaceous oceans were characterized by warm saline deep water originating in low latitudes experiencing high evaporation (Gale 2000; Kidder & Worsley 2010; Hay & Flügel 2012).

The Cretaceous is a unique period in displaying this combination of familiar and alien characteristics. Adding the fact that it is the oldest period in which plate tectonic reconstructions are constrained by seafloor magnetic spreading, and that its sedimentary rock record is widespread and abundant, it is an ideal time interval to study global climate change through deep time (Spicer 2003; Hay 2008). Considering that this interval had a longer duration than the entire Cenozoic era, an investigation of the effects of environmental change on marine or terrestrial biota that could be relevant to our contemporary challenges should focus on a shorter time span.

The Cenomanian (100.5 – 93.9 Ma) is the oldest stage of the Late Cretaceous (Cohen *et al.* 2018) and presents a combination of suitable conditions for this investigation, such as rapid global warming, highly fluctuating sea levels, and marked faunal and floral turnovers. Most of the Cretaceous ranks among the ‘greenhouse’ phases of geological history, with global average temperatures oscillating between 20°C and 30°C (Hay & Flögel 2012). However, the Cenomanian represents one of the ‘hothouse’ intervals, with a sharp CO₂ increase leading to a thermal maximum with global averages reaching and perhaps exceeding 40°C (Bice *et al.* 2006; Hay & Flögel 2012)! The mechanism behind this CO₂ incursion may be a 50 – 70% increase in the pulse of ocean crust production in the Pacific between 120 Ma and 80 Ma (Larson 1991). This same mechanism is probably responsible for the record sea levels registered at the Cenomanian-Turonian boundary (Gale 2000; Skelton 2003; Haq 2014). Although a rising or falling sea level trend can be detected on a 10⁷ year scale, studies of marine successions in chalk facies reveal far more frequent fluctuations in the short term across the entire Cretaceous, revealing the rapid transgressions and regressions of epicontinental seas such as the Western Interior Seaway (Koch & Brenner 2009; Haq 2014). In the deeper ocean, warmer water led to anoxic conditions that were probably the main cause of the ‘Mid-Cretaceous minor extinction event’ (Gale 2000; Hay 2008; Kidder & Worsley 2010).

On land, the Cenomanian lies in the middle of the Cretaceous Terrestrial Revolution, one of the most consequential biotic turnovers for the dynamics of contemporary terrestrial ecosystems. It is during this interval that the specific richness of angiosperms (and probably their functional and ecological diversity) first surpassed that of gymnosperms, and that angiosperm trees first evolved (Wing & Boucher 1998; Lupia *et al.* 2000; Coiffard *et al.* 2012). This floral turnover likely had a knock-on effect on the most diverse and abundant primary consumers of trophic networks, with the diversity of insect lineages with dominant angiosperm hosts increasing sharply at the expense of the diversity of lineages with fern or gymnosperm hosts (Labandeira 2014, 2018).

This review examines the environmental trends of terrestrial ecosystems around the middle of the Cretaceous. Evidence from a variety of palaeoclimate indicators is discussed for each of the planet’s main biomes, complemented by an overview of angiosperm diversity represented by fossil floras. The last part of the review brings greater focus to insect diversity trends, using evidence from compression and impression fossils and amber inclusions.

1.2.2 *Terrestrial palaeoclimate indicators in the rock record*

Most models of Cretaceous climates at the global scale have used $\delta^{18}\text{O}$ isotope and/or Mg/Ca ratios recovered from planktonic foraminifera as a sea-surface temperature indicator (Gale 2000). They generally agree in demonstrating an overall temperature rise from the Barremian to the Albian-Cenomanian, then a peak during a Cenomanian-Santonian interval, followed by a fall towards the latest Cretaceous (Bice *et al.* 2006; Gale 2000: 14). However, the marine origin of these proxies limits the extrapolation of their results to terrestrial ecosystems. Contrary to marine ecosystems, terrestrial ecosystems are directly exposed to atmospheric conditions, which means that their climate changes at higher spatiotemporal resolutions, especially in continental interiors (Spicer 2000, 2003). This is compounded by the fact that isotopic composition may be affected by diagenetic changes (Spicer 2003). In these cases, the study of climate-sensitive fossils and sedimentary rocks usually provides a more local or regional glimpse into an ecosystem in space and in time.

Lithological climate proxies consist in sedimentary rocks that result from diagenetic processes that have occurred under particular environmental conditions. For instance, the occurrence of coal deposits is indicative of a humid climate where precipitation exceeds or is equal to evaporation, and where organic matter can be accumulated in anoxic conditions (Parrish *et al.* 1982; Craggs *et al.* 2012). In contrast, evaporites such as gypsum, anhydrite and halite accumulate in basins where evaporation exceeds precipitation, marine or river influx, and runoff combined, and indicate hot arid climates (Craggs *et al.* 2012). Laterites and bauxites result from the subaerial chemical weathering of iron-rich rocks under high annual rainfall, high humidity and high mean annual temperatures (Craggs *et al.* 2012). These are broad categories of the most common lithological climate indicators.

The recognition of biological climate proxies in the fossil record can be considered a consequence of inferences on the ecology of extinct species in attempts to reconstruct ancient ecosystems (Damuth 1992; Wing & DiMichele 1992). These inferences are usually based on some of the following uniformitarian principles: ‘taxon-free’ inferences based on functional morphology assume that animals or plants with a similar morphology necessarily have a similar physiology, and thus similar climate preferences (Wing & DiMichele 1992; Wing & Greenwood 1993; Tiffney 2008). In contrast, taxonomic inferences are based on the ecological preferences of the nearest living relatives (NLR) of an extinct species or taxon (Wing & Greenwood 1993). They assume

that (1) there is indeed a close relationship between a given extinct species and this living relative; (2) that the lineage containing the fossil and its living relative contains little evolutionary change susceptible of leading to change in ecological preferences; and (3) that the extant species' range is constrained entirely by abiotic factors (such as climate) and not by biotic factors (such as competition) (Wing & DiMichele 1992). As a result, NLR methods are considered to have very high uncertainties prior to the Quaternary, since evolutionary stasis is very unlikely in an old lineage under selection pressure from environmental change in deep time (Spicer & Axelrod 1990). Bioclimatic analysis at least provides quantitative estimates, which means it is not restricted to organisms that have obvious qualitative climate preferences such as palms or crocodilians (Wing & Greenwood 1993). This method consists in an estimation of clearly defined climate parameters (such as mean annual or cold month mean temperature) for fossil species based on the climate tolerance of their nearest living relatives (Kershaw 1997; Greenwood *et al.* 2005). Despite being applicable to a wide range of plant remains, from fern, cycad and conifer leaves to spores and pollen (Kershaw & Nix 1988; Fletcher *et al.* 2014), it remains hampered by the assumptions outlined above.

Inferences from functional morphology are not constrained by these conditions, and they directly account for the influence of natural selection in directing the evolution of populations to their environment, providing insight on multiple cases of convergence in the process (Wing & DiMichele 1992). Palaeobotanical studies on fossil leaves are a well-known application of such taxon-independent ecological inferences. Throughout their evolution, plant populations have been subject to universal selection pressures based on mechanical and physiological constraints in favour of phenotypes that display a maximization of photosynthetic capacity while minimizing water loss and energy investment in structure and gas exchanges (Givnish & Vermeij 1976; Spicer 2000).

In order to obtain insight on past climates, these two uniformitarian methods of inference are best applied together on organisms whose physiology is relatively well understood, and that are known to have specific climatic preferences. A classic example is the case for the prevalence of warm, humid and equable Palaeocene and early Eocene climates based on the fossil occurrences of thermophilic organisms such as palms, turtles and crocodilians (Wing & Greenwood 1993; Markwick 1998; Greenwood *et al.* 2005), some of which have been found in the High Arctic (Dawson *et al.* 1976; Estes & Hutchison 1980). A rare attempt at a quantitative estimate based on

an animal came in the description of the giant boid *Titanoboa cerrejonensis* Head et al., 2009 from the Palaeocene of Colombia.

When quantitative estimates are needed, angiosperm tree leaves are the most widely used biological climate proxy. These structures have a higher morphological diversity than in other plant taxa, and they have a higher level of phenotypic plasticity in response to environmental conditions (Spicer 2000). Among angiosperms, woody dicots have the most consistent response (Wolfe 1993; Spicer 2006; Li *et al.* 2016). The first of these relationships to be detected in extant floras was a positive correlation between the percentage of species with untoothed tree leaf margins and their habitat's MAT (Bailey & Sinnott 1915, 1916). Regressions plotted from extant floras could then be used to infer MAT in deep time based on that same proportion in fossil floras, in a method called leaf margin analysis (LMA) (Wolfe 1979; Wilf 1997; Greenwood 2007). This was the basis for the detection of more correlations between leaf physiognomic characters and climate parameters, such as the positive correlation between leaf size and precipitation (Wolfe 1978, 1993; Wolfe & Upchurch 1987). Together, they form the Climate Leaf Analysis Multivariate Program (CLAMP), introduced by Wolfe (1993) and later refined with more studies on the influence of taphonomic loss and uncertainties in temperature and precipitation (Spicer 2006; Dilcher *et al.* 2009; Spicer *et al.* 2011; Yang *et al.* 2011, 2015) (see Chapters 2 and 4 for details). This model offers more local palaeoclimate information and acknowledges a far larger influence of climate on leaf physiognomy. Sufficiently precise quantitative temperature and precipitation estimates also enable the positioning of a given fossil assemblage into one of the climate zones of the Köppen-Geiger classification system (Kottek *et al.* 2006). At the moment, CLAMP remains the most precise and accurate method for the quantitative estimation of palaeoclimates in continental interiors where data from the rock record is not directly comparable to oxygen isotope data collected from marine sediments (Spicer 2003).

Whichever uniformitarian assumption is used, the major disadvantage of biological climate indicators is that they can only be applied to time intervals populated by extinct organisms that have a similar morphology or physiology to extant organisms. The corollary is that these methods are ever less likely to be suitable for older assemblages that generally have a lower diversity of familiar species. For example, the use of leaf physiognomy for quantitative climate estimates such as CLAMP is restricted to the last 100 Ma (Spicer 2003, 2006), since (1) only woody angiosperm leaves demonstrate a consistent physiognomic response to climatic conditions (Wolfe 1979, 1993),

and (2) no clear fossil evidence for woody angiosperms has been found prior to the Cenomanian (Lupia *et al.* 2000; Philippe *et al.* 2008; Feild *et al.* 2011). It cannot be used for such a long span of geological time as bioclimatic analysis, yet its bias is lesser because it does not rely on NLR assumptions.

Other palaeoclimate reconstruction methods based on vegetation use the palynoflora and/or the structure of fossil wood. The accurate description of pollen and spores can lead to the identification of the source plants, providing a glimpse into a floral assemblage that becomes ever more vital when the macroflora is insufficiently preserved (Muller 1981). Palynostratigraphy can also be useful for the relative dating of sedimentary units when the lack of suitable isotopes renders radiometric dating impossible (Spicer 2003). However, palynofloral analyses have major disadvantages: (1) the higher robustness of pollen and spores relative to macrofloral remains implies they can be reworked from older sediments, reducing spatial and temporal resolution, and (2) different amounts of pollen produced by different source plants may lead to sampling bias in abundance and diversity estimates (Spicer 2003). As an example, Lupia *et al.* (2000) suggested low angiosperm pollen production compared with gymnosperm productivity to explain their strange results for Cenomanian plant diversity, which showed a very high disparity in angiosperm frequencies out of total diversity between palynofloras (30%) and macrofloras (60 – 80%). Thus, the morphological disparity observed within a pollen sample is often lower than the actual floral diversity of a given locality (Crabtree 1987). These uncertainties are particularly high for very old floras (such as those of Cretaceous age) containing far fewer extant genera, and whose age is often poorly constrained, which could be an additional source of error in Lupia *et al.* (2000).

Palaeoecology offers more direct information on the temperature, precipitation and seasonal cycle of extinct ecosystems. Similar to angiosperm leaf physiognomy, woods belonging to distantly related lineages, but evolving under similar selection pressures, present convergent features in their structural anatomy (Carlquist 1977; Wolfe & Upchurch 1987). Old trees have a record of annual growth rings, which are more clearly defined in environments with a marked seasonality (Creber & Chaloner 1985). If a distinction between early wood (with large xylem cells) and late wood (with cells decreasing in size) is possible, it means that tree growth occurred partly during an unfavourable period, with insufficient photoperiod and/or precipitation (Wolfe & Upchurch 1987). Conversely, a relatively wide band combined with a higher proportion of early wood indicates a long and favourable growing season.

The following section reviews evidence from the palaeoclimate indicators summarized in the preceding paragraphs to produce an overview of the main climate zones, and consequently the main biomes, that defined terrestrial ecosystems in the middle of the Cretaceous.

1.2.3 Climatic zones and vegetation in the middle of the Cretaceous

The climate proxy data accumulated from various localities of similar age can be reunited to produce palaeogeographic maps. The location of climate-sensitive plants or sediments can lead to inferences on roughly delineated climatic belts (Boucot *et al.* 2013). The most ambitious of these maps form a series of planispheres for almost each age of the Cretaceous: not only were climatic belts superimposed on locations of fossil and sedimentary proxies, but the inclusion of precipitation regimes led to the delineation of vegetation zones (Chumakov *et al.* 1995). This makes the Chumakov maps an indispensable reference to subsequent studies on Cretaceous climate, geography, and ecology (Spicer & Skelton 2003; Craggs *et al.* 2012; Hay & Flögel 2012).

The Cenomanian map, for instance, displays an equatorial humid zone at the lowest latitudes, flanked by hot arid zones and evaporite belts (Fig. 1). Warm humid belts occupy middle latitudes, and high latitudes are occupied by temperate humid belts almost all the way to the poles. The remainder of this section will examine in greater detail the fossil and sedimentary evidence for this very high climatic equability across the latitudinal gradient. The gathering of climate proxy data for time bins lasting many millions of years each inevitably leads to analytical time-averaging, in which some events of short to mid-term environmental change could be obscured (Behrensmeyer & Hook 1992: 74-76). Limitations in the rock record and high dating uncertainties of the majority of this record prevent us from reaching a higher temporal resolution at such deep time scales.

Low latitudes: the humid equatorial and hot arid zones

Unsurprisingly, the Cenomanian world was at its hottest in the tropics. Earth's lowest 30 – 40° were occupied by an equatorial humid zone flanked by arid zones on either hemisphere, which is supported by the widespread occurrence of evaporites such as gypsum and anhydrite (Chumakov *et al.* 1995; Russell & Paesler 2003; Fig. 1). It is further supported by the detection of a wide *Classopollis* zone (a pollen indicative of dry conditions) stretching approximately between 40°N and 40°S (Spicer & Skelton 2003). Together, these sources independently support the estimation

of sea-surface temperatures reaching 33 – 34°C in the tropical western North Atlantic based on foraminifera-derived oxygen isotopes (Norris *et al.* 2002).

A more humid equatorial climate is detected at the very lowest latitudes by the occurrences of coals, bauxites and laterites, mainly from the south of the Sahara Desert (Spicer & Skelton 2003). However, there is no palaeobotanical evidence for an equatorial forest belt equivalent to that of the late Cenozoic. The extremely high temperatures at low latitudes would have induced evaporative stress and droughts, which would generally lead to more xeric forests than in northern latitudes (Spicer *et al.* 1996; Gale 2000). For instance, the southern half of the Sahara was a vast floodplain stretching from the Atlantic to the Tethys, presenting an alternation of wet and arid facies on thousand-year time scales (Russell & Paesler 2003). In what is now Niger, clays would have washed into an epicontinental sea that isolated West Africa, indicating sporadic rainfall (Russell & Paesler 2003). In general, palaeobotanical proxies suggest a highly seasonal climate, with fossils indicating the presence of an open woodland dominated by ferns and cycads (Spicer & Skelton 2003).

Despite the suggestion that extremes in CO₂ and temperature would have affected the evaporative and thermoregulatory mechanisms of animals and plants at these latitudes, the fossil record shows an abundance of life, especially in freshwater settings (Russell & Paesler 2003). The Echkar Formation, for instance, presents a glimpse into the equatorial occupants of the vast floodplain that covered much of northern Africa: it presents a morphologically diverse crocodyliform fauna, including the amphibious flat-skulled *Laganosuchus* Sereno & Larsson 2009, the small terrestrial *Araripesuchus rattoides* Sereno & Larsson 2009, and *Kaprosuchus* Sereno & Larsson 2009 with its hypertrophied dentition. These are joined by an array of fish and Gondwanan dinosaurs, including titanosaurs and theropods such as *Carcharodontosaurus* and the ancestral abelisaurid *Rugops* (Sereno *et al.* 2004; Brusatte & Sereno 2007), and the sail-backed iguanodontian *Ouranosaurus* (Russell & Paesler 2003).

The only regions containing fossil evidence for equatorial forests in the Cenomanian are northwestern South America and Southeast Asia. The Colombian Cretaceous rock record contains shallow marine shales with organic material derived from highly productive land vegetation (Spicer & Skelton 2003). The other key locality is the Hukawng Valley, Kachin State, Myanmar, which contains the richest amber deposit of the entire Cretaceous (Grimaldi *et al.* 2002; Ross 2019a, b). A Cenomanian age based on zircon dating for the amber is widely accepted (Shi *et al.*

2012). However, traces of re-deposition suggest the amber was formed in the late Albian, closer to an anterior dating estimate based on ammonite assemblage zones and palynomorphs (Cruickshank & Ko 2003). Since 2000, the number of species described from this locality has risen exponentially from 60 to 1300, 1223 of which are arthropods (Ross 2018, 2019a).

The high abundance and diversity of plants and animals with remarkable soft-tissue preservation in Burmese amber provides additional morphological characters for resolving phylogenies, as well as insight on biogeographical problems for many lineages. Although lower latitudes are widely considered to have witnessed the evolution of angiosperms in the Early Cretaceous, the evidence is most often limited to pollen (Axelrod 1959, 1970; Crane & Lidgard 1989). In this respect, the palaeobotanical record of Burmese amber is indispensable for tracing this evolution, since it is one of the few low-latitude localities to preserve complete early flowers (Crepet *et al.* 2016; Poinar *et al.* 2016; Liu *et al.* 2018). A different biogeographical question can be addressed with *Cretoperipatus burmiticus* Grimaldi *et al.*, 2002, the oldest and only pre-Cenozoic onychophoran in the fossil record, which is key to understanding the arrival of the Gondwanan lineage Peripatidae in Southeast Asia (Oliveira *et al.* 2016). *Chimerarachne yingi* B. Wang *et al.*, 2018 is a spider that displays a segmented opisthosoma with an elongated telson characteristic of ancestral Uraraneida, while displaying spinnerets characteristic of modern Mesothelae. A tick wrapped in spider silk represents a rare capture of such a predation event in the fossil record (Dunlop *et al.* 2018).

In terms of vertebrates, this locality contains the oldest lizard assemblage preserved in amber (Daza *et al.* 2016), the oldest occurrence of anurans in humid tropical forests (Xing *et al.* 2018a), and the first Mesozoic snake found in a tropical environment (Xing *et al.* 2018b). A particularly remarkable piece contains a partial juvenile coelurosaur tail with a rare case of three-dimensional plumage associated with skeletal material, offering unique insight on the evolution of feathers (Xing *et al.* 2016a). Even closer to modern birds, the enantiornithine record has been greatly expanded by the discovery of precocial wings (Xing *et al.* 2016b), fully feathered feet (Xing *et al.* 2019a), a new genus with a uniquely elongated third pedal digit (Xing *et al.* 2019b), and even an articulated hatchling preserved in a particularly large amber specimen (Xing *et al.* 2017). The extremely fast pace of these discoveries across almost all major tropical forest taxa suggests that it is only a matter of time before an arboreal mammal is found in Burmese amber.

During the Cenomanian, Myanmar would have been part of the West Burma Block, an island drifting northward across the eastern Tethys (Poinar 2018). This means that the palaeolatitude of this amber locality would probably have been lower than today, and that many of its species may have been endemic to this landmass due to evolution in isolation. Together, these organisms offer a unique window into Cretaceous equatorial forest communities. The regional occurrence of these forests may have been caused by an increase in low-latitude humidity that came with sea level rise, and the latter's local availability due to suitably directed winds (Spicer & Skelton 2003).

The only localities in the desert-dominated evaporite belts to have a similarly high diversity to the humid equatorial zone contain sediments that were deposited in fluvio-deltaic settings. A megafloora from the Bahariya oasis of Egypt, of which 25 of the 30 morphotypes were angiosperms, contains a high number of small entire-margined leaves, suggesting a hot and dry climate even in a less arid environment (Lyon *et al.* 2001). The fish fauna preserved in the Kem Kem beds of Morocco contains a high diversity of large species such as lungfish, as well as sawfish such as *Onchopristis* and some of the oldest cladistians related to *Polypterus* (Dutheil 1999; Cavin *et al.* 2015). These would have supported more crocodyliforms such as *Elosuchus* and *Hamadasuchus* (Larsson & Sues 2007; Meunier & Larsson 2017), as well as gigantic theropods such as *Spinosaurus aegyptiacus* (Läng *et al.* 2013).

Some climate models have proposed that the extremely high CO₂, temperature, and sometimes humidity, levels characteristic of the Cenomanian tropics would have posed a challenge to plant and animal life, either through heat stress or by impeding thermoregulatory mechanisms (Hay & Flögel 2012). However, these models fail to acknowledge a fossil record that reveals thriving freshwater and terrestrial communities at these low latitudes (Russell & Paesler 2003), and simultaneously fail to acknowledge the response of similarly rich communities that evolved during other hothouse events, such as the Palaeocene-Eocene Thermal Maximum (Wing *et al.* 2005; McInerney & Wing 2011).

Middle latitudes: the warm humid subtropical to temperate zones

An equable latitudinal temperature gradient does not preclude a steep latitudinal precipitation gradient, as noted by Gale (2000). High evaporation rates at low latitudes would have induced a poleward moisture transport, leading to higher precipitation at mid to high latitudes.

This means that plant productivity in the Cenomanian was concentrated at these middle latitudes, which combined sufficiently high precipitation rates with a sufficiently long photoperiod.

North America and Europe currently offer the most complete angiosperm megafossil record for an age that witnessed key developments in their ecological expansion, notably the evolution of large angiosperm trees (Wolfe & Upchurch 1987; Kvaček & Dilcher 2000; Coiffard *et al.* 2012). Conversely, it means that the northern warm humid zone has the largest CLAMP dataset for the Cenomanian. Quantitative analysis of these floras yield mean annual temperatures between 15°C and 20°C, temperatures for the warmest month usually above 20°C, and temperatures for the coldest month usually between 8°C and 11°C, far above freezing (Wolfe & Upchurch 1987; Miller *et al.* 2006; Spicer & Herman 2010). Together with sedimentary proxies such as kaolinite (Austin 1970), these palaeobotanical proxies suggest that subtropical climates, with almost no freezing period, extended to at least 60° in latitude (Chumakov *et al.* 1995; Fig. 1).

Many North American megafloras contain a high abundance of leaves belonging to large size classes, with cordate bases and drip tips, all of which are adaptations now found in regions that experience warm humid climates (Wolfe & Upchurch 1987). These characteristics are found in floras across the entire continent, from the Raritan Formation and Amboy Clays on the eastern seaboard (Newberry & Hollick 1886; Berry 1910), to the Dakota floras along the Western Interior Seaway (Lesquereux 1892; Wang & Dilcher 2018), to the Winthrop and Dunvegan floras along the American cordillera (Crabtree 1987; Miller *et al.* 2006), and suggest the prevalence of warm temperate to subtropical forests at these latitudes.

Europe is represented by fewer leaf megafloral sites, most notably the Peruc flora of the Czech Republic, which was second only to the Dakota flora in Cenomanian floral diversity (Kvaček & Dilcher 2000). Its coastal location on the Bohemian Massif island in the Tethys makes it one of the few floras from which palaeoclimate predictions can be directly compared with isotope data (Spicer 2003). This continent also contains a relatively high number of fossil wood localities, which contain some of the oldest angiosperm tree remains (Philippe *et al.* 2008). The southern warm humid zone is largely represented by floras in the Mata Amarilla Formation, Patagonia (Iglesias *et al.* 2007), and the Winton flora of Queensland, Australia (McLoughlin *et al.* 1995). Being on the shores of the epicontinental Eromanga Sea that split Australia in half, the Winton flora would have had a similar climate and depositional setting to North American and European floras (Fletcher *et al.* 2014).

A few floras may reveal exceptions to this prevalent warm humid climate. Some sites from the southeastern United States, such as Alabama's Tuscaloosa Formation, are dominated by leaves belonging to evergreen trees, with woods presenting almost no growth rings (Wolfe & Upchurch 1987). Low leaf size indicative of low to moderate precipitation, indicating an open canopy forest in turn. Generally xeric conditions combined with a lack of any pronounced wet or dry season are exceedingly rare today, with the closest modern analogue being New Caledonian open forests (Wolfe & Upchurch 1987).

Angiosperm dominance in more disturbed, well drained riparian and coastal settings was already well established by the Albian, as shown by work on the Potomac Group of the mid-Atlantic seaboard (Doyle & Hickey 1976; Hickey & Doyle 1977). The localities of the Dakota Formation that are of definite Cenomanian age display the highest floral diversity of their time and had an alluvial floodplain as their depositional environment (Wang & Dilcher 2006a). The Rose Creek site contains some of the oldest angiosperms accustomed to brackish water (Upchurch & Dilcher 1990), as well as peltate-leaved aquatic species (Wang & Dilcher 2006b) and some of the earliest flowers with distinct sepals and petals (Basinger & Dilcher 1984). One locality even seems to contain some of the oldest mangrove forests (Wolfe & Upchurch 1987). Additional support for angiosperm dominance of the Dakota Flora comes from the demonstration of a more inland origin for the only conifer spores to be found in the formation (Retallack & Dilcher 1981, 1986). The detection of rapid sea-level fluctuations in the Dakota Formation throughout the Albian and the Cenomanian (Koch & Brenner 2009), coupled with the almost absolute dominance of angiosperms in this unit, supports the hypothesis of an angiosperm radiation favoured by increasingly unstable environmental conditions that were caused by the advent of the Cenomanian-Turonian hothouse event.

However, it remains uncertain whether there was a general trend of undisturbed habitat colonization this early in angiosperm evolution, or whether they simply took advantage of an expansion of their preferred disturbed settings as temperatures and sea levels rose. The discovery of a megafloora with medium-sized leaves in Labrador, near the northern limits of this zone, led to suggestions that the landscape was covered by 'a lush vegetation, more or less similar to actual forests of New England' (Blais 1959). Their occurrence along ferns and conifers in such an inland locality, apparently far from any disturbed setting, may suggest the occupation of new habitats. In other sites, such as Utah's late Albian Soap Wash flora, the lone occurrence of angiosperms

coupled with the absence of ferns and conifers suggests a local angiosperm invasion of a more disturbed setting (Arens & Harris 2015). However, little more can be concluded from these two local floras unless more coeval sites are found in their vicinity.

Whatever the timing of the angiosperm radiation, it was probably influenced by a very high fire frequency characteristic of the Cretaceous as a whole, which can be detected by the global abundance of charcoal in the lithological record (Bond & Scott 2010). The entire period is characterized by physical conditions favourable to fires, such as high temperatures, seasonally dry climates and a higher O₂ content. For instance, the widespread occurrence of fusainized specimens of the fern *Weichselia* throughout Early Cretaceous Europe may represent a case of a community being maintained by frequent wildfires (Spicer & Skelton 2003). Angiosperms have been shown to accumulate flammable biomass more rapidly than other plants, which could have induced a positive feedback with the initiation of new fire regimes during the Cretaceous (Bond & Scott 2010; Brown *et al.* 2012). Their higher growth rates would also have enabled them to make the most of increased nutrient supply more readily than gymnosperms while producing litter that is more easily decomposed, promoting an increased nutrient release (Berendse & Scheffer 2009). It is interesting to note that the Cretaceous interval that is at the fulcrum of the angiosperm radiation (Albian-Cenomanian) is also the interval that experiences synchronous rises in O₂ and CO₂ concentrations. This may have significantly increased the intensity of fire regimes (Brown *et al.* 2012), which in turn may have driven this positive feedback with angiosperm growth. If a causality between fire intensity and angiosperm abundance and/or diversity is further confirmed, it would lend much credence to Court Jester hypotheses favouring changes in the physical environment as the main drivers of the Cretaceous Terrestrial Revolution (Benton 2009).

High latitudes: the temperate humid zones

During the Cenomanian hothouse, temperate climates were limited to the polar and subpolar regions. Contrary to today, forests extended to the highest continental latitudes and are represented by leaf megafloras, woods and coals (Spicer & Parrish 1986; Fig. 1). Diverse floras have been reported all around the poles, especially on Alaska's North Slope and in eastern Russia (Spicer *et al.* 2008; Spicer & Herman 2010). These landmasses would have occupied even higher palaeolatitudes than at present, with the northern reaches of Russia and Alaska exceeding 80°N in latitude (Spicer & Herman 2010). Despite an unprecedented latitudinal climate equability, the

extreme low-light conditions it entails would have severely limited the photoperiod and growing season, with knock-on effects on the animal biomass these forests could support (Herman *et al.* 2016; Spicer *et al.* 2019).

Since these ecosystems span the entire Late Cretaceous and evolved under environmental conditions that have no analogue today, they offer a rare opportunity to study the evolution of polar forests in deep time (Spicer & Parrish 1986; Spicer & Herman 2010). For instance, the study of conifer wood cell structure has revealed extreme seasonality between benign and unfavourable growing conditions (Herman *et al.* 2016). Cycads and conifers differed markedly from extant relatives by bearing deciduous foliage as an adaptation to low-light conditions for a dormancy period that could easily last one third of the year (Spicer & Parrish 1986; Parrish & Spicer 1988). While angiosperms were already well established by the Albian at lower latitudes (Crane *et al.* 1995), their earliest record at polar latitudes is as late as the Cenomanian Nanushuk flora from the North Slope of Alaska (Spicer & Herman 2010). The fact that angiosperms are detected so late in the Cretaceous at these high latitudes may support their origin at lower latitudes. After the Albian-Cenomanian, floral diversity in the North Slope drops from ~67 morphotypes to ~10 morphotypes in the Campanian-Maastrichtian (Parrish & Spicer 1988). Considering that palaeolatitude (and therefore the extreme light regime) did not change significantly throughout the Late Cretaceous, this trend can be explained by a gradual cooling after the Cenomanian-Turonian thermal maximum, where mean annual temperatures drop from 13 – 14°C to 7 – 10°C (Parrish & Spicer 1988; Spicer & Herman 2010). Harsher growth conditions in the latest Cretaceous are demonstrated by frequent interruptions during the growth period of Maastrichtian wood when temperature fell below 10°C (Herman *et al.* 2016).

The Vilui Basin's Timerdyakh Formation in central Siberia remains the Cenomanian site with the lowest mean annual temperature estimated from CLAMP (~13°C), yet its cold month mean temperature remained above freezing (5.5°C) (Spicer *et al.* 2008). Even at a time of high sea levels, this basin would have been deep in a continental interior at a latitude around 72°N, yet it presents traces of smectite and kaolinite that would have indicated a warm humid climate at least locally (Spicer 2003). The Grebenka flora, near the eastern extremity of Russia, has similar CLAMP results and still presents one of the highest floral diversities reported from any Cenomanian site (Spicer *et al.* 2002, 2019; Spicer 2003). Studies of these very cool localities show

that subpolar forests still enjoyed a relatively equable climate in spite of a challenging light regime for vegetation growth.

The southern temperate humid zone contains only a few mixed angiosperm-gymnosperm floras, such as that of the Matakaea Group of Eastern Otago, New Zealand (Pole 1992). Climate estimates based on the nearby Clarence Valley flora suggest New Zealand may have had a mean annual temperature as low as 10°C, with a climate and a light regime analogous to that of the Russian and Alaskan polar forests (Parrish *et al.* 1998; Spicer & Skelton 2003). Antarctica's Alexander Island also has a few leaf megafossils of estimated Albian age (Cantrill & Nichols 1996), as well as wood showing that the region was at the peak of a cooling event towards the end of the Albian, in contrast with other parts of the world (Francis & Poole 2002). However, a data gap extending until the Campanian prevents us from drawing stronger conclusions.

The temperate humid belts were the only Cenomanian climate and vegetation zone for which organic accumulation leading to the formation of peats and subsequently coals exceeded oxidation by fires. This was largely due to sufficiently high precipitations that led to silicate weathering, inducing carbon sequestration in turn (Spicer & Skelton 2003). Even at such high latitudes, temperatures could drop to such an extent that silicate weathering would be impeded in the winter, which contributes to a globally low carbon sequestration rate in the middle of the Cretaceous (Spicer & Skelton 2003).

1.2.4 Evolution of insect diversity in the middle of the Cretaceous

A summary of environmental trends in the Mesozoic or Cenozoic cannot be complete without mentioning the role of insects. Today, these are the dominant animals in terrestrial ecosystems, in terms of species richness as well as biomass and influence on ecosystem productivity (Grimaldi & Engel 2005). Insects are by far the main plant consumers and pollinators in modern ecosystems, and an ever-expanding fossil record over the last 30 years shows that they would have exerted a similarly high influence on Mesozoic ecosystems.

The middle of the Cretaceous (generally the Albian-Turonian interval) bears a particular biological significance for the evolution of the present insect diversity. It is one of the ages of origination for many recent families (including many ecologically dominant eusocial insect lineages), at a time when angiosperms definitely seem to start their ecological expansion (Labandeira 2014). It is also a time of very high sea levels that increase the isolation of islands and

larger landmasses (potentially promoting endemism), and it is the age of the most biodiverse amber deposits of the entire Cretaceous, located in Myanmar (Grimaldi *et al.* 2002; Ross 2019b, a).

Burmese amber contains the vast majority of insect diversity currently known from the Cenomanian: as it stands, 925 species are divided into 379 families (the latter rising to 508 families if all arthropods are included) (Ross 2019a). The only other sites with a significant number of insect fossils for this age are restricted to the Charentes and Anjou amber deposits from southwestern France (82 arthropod families altogether) (Perrichot 2003), as well as the Agapa amber from the Dolgan Formation in the Taimyr Peninsula, Siberia (42 arthropod families) (Rasnitsyn *et al.* 2016). Among earlier insect lagerstätten, the closest in time include the highly prolific Crato Formation of Brazil (Grimaldi 1990; Barling *et al.* 2015) and the Koonwarra lacustrine deposits, Queensland, Australia (Jell & Duncan 1986) (both Aptian), and Albian amber from Cantabria and Aragón, Spain (Delclòs *et al.* 2007). Later lagerstätten (from the Turonian-Coniacian) include New Jersey amber (Grimaldi *et al.* 2000), mudstone lenses in the fluvial deposits of Kzyl-Zhar, Kazakhstan (Zherikhin 2002), and the crater lake deposits of Orapa, Botswana (Rayner *et al.* 1997).

As plants underwent a significant turnover in the middle of the Cretaceous, so did insects. Most of that insect turnover seems driven by the capacity (or lack thereof) to adapt to new food and pollinating sources in flowering plants. Notable extinctions among gymnosperm pollinators include lineages characterized by very long proboscides, such as mecopterans (scorpionflies) and kalligrammatids, as well as beetles, orthopteroids and melanthripid thrips (Ren *et al.* 2009; Labandeira 2010). Many hemipteran lineages also seem to go extinct, notably Palaeontinidae as the last non-clypeate cicadomorphs (Szwedo 2018).

By contrast, insect lineages associated with angiosperms either increased in diversity or originated altogether at this time. Among these, 60 families seem to have shifted their host preference from gymnosperms to angiosperms, including many brachyceran flies, plant-hoppers (Fulgoroidea) and scale insects (Coccoidea) (Labandeira 2014; Veá & Grimaldi 2016; Szwedo 2018). These are joined by the first occurrences of many glossatan lepidopterans, parasitoid apocritan wasps, thripid thrips, and various coleopteran lineages (Grimaldi 1999). Phylogenetic approaches systematically recover a sharp overall rise in insect diversity, which seems largely driven by dipterans, hymenopterans and lepidopterans co-evolving with angiosperms (Grimaldi & Engel 2005; Wahlberg *et al.* 2013; Misof *et al.* 2014; Peters *et al.* 2017). Molecular phylogenies

have shown that repeated origins of lineages feeding on angiosperms were systematically associated with adaptive radiations and higher diversification rates (Farrell 1998; Wiens *et al.* 2015). However, these general trends are partially challenged at higher taxonomical resolutions: for instance, the origin of some genera of pygmy leaf-mining moths (Nepticulidae) was dated to the Early Cretaceous, long before the accepted age of the angiosperm radiation (Doorenweerd *et al.* 2017). As another example, the origin of leaf beetles (Chrysomelidae) was dated to 73-79 Mya, ~10 Ma after the end of the angiosperm radiation (Gómez-Zurita *et al.* 2007).

Most of the fossil evidence for insect pollination or herbivory on angiosperms in the Cretaceous is indirect, meaning that it does not preserve a tangible interaction between the animal and the plant. The amber record is particularly rich in three indirect lines of evidence (Grimaldi *et al.* 2000, 2019; Grimaldi & Engel 2005; Labandeira 2010): insects with anthophilous characters (such as a long proboscis); (2) fusainized flowers with entomophilous characters; and (3) relatives of extant pollinators that are assumed to share a pollinating habit (following Nearest Living Relative assumptions). However, these are not sufficient to accurately trace the insect-angiosperm co-evolution. As explained by Grimaldi *et al.* (2019), they do not enable the detection of pollinators among taxa lacking significant anthophilous traits that would probably have had a more generalized pollination syndrome, leading to underestimations of the past diversity of anthophilous insects. This is corroborated by compilations of various extant and extinct lineages that show that very closely related families (in hemipterans, for instance) could have very different host plant preferences (see mentions of Brachycera, Fulgoroidea and Coccoidea in previous paragraph). For many years, the only direct sources of evidence for insect pollination were amber inclusions containing an insect alongside gymnosperm pollen grains, often localized around the legs and mouthparts. The oldest of these traces are xyelid sawflies from the Early Cretaceous locality of Baissa, Siberia (Krassilov *et al.* 2003). Similar associations have also been reported for thrips from Early Cretaceous Spanish amber (Peñalver *et al.* 2012) and for boganiid beetles feeding on cycad pollen in Burmese amber (Cai *et al.* 2018). In contrast, the earliest corresponding evidence for angiosperm pollination was previously known from the extinct bee tribe Electrapini, from the Eocene lagerstätte of Messel (Wappler *et al.* 2015). Only recently has the age of the oldest direct evidence for insect-angiosperm pollination been pushed back to the middle of the Cretaceous. Eudicot pollen grains have now been independently discovered in two different inclusions from Burmese amber, one containing the tumbling flower beetle (Mordellidae) *Angimordella burmitina*

(Bao *et al.* 2019) and another containing the basal aculeate wasp *ProspheX anthophilos* (Grimaldi *et al.* 2019). Together, these amber inclusions definitely confirm that insects pollinated angiosperms at least as early as the earliest Cenomanian, at the height of the Cretaceous Terrestrial Revolution.

Despite these demonstrations of actual pollination behaviour with individual fossils and synchronous radiations with entire fossil datasets, the ecophysiological mechanisms underlying a possible insect-angiosperm co-evolution remain unclear. Considering that pollination by insects would almost certainly enable a given angiosperm population to occupy a larger territory than a wind-pollinated population of similar size, insect diversification may have triggered yet another positive feedback favouring the angiosperm radiation (Grimaldi & Engel 2005). A recent hypothesis suggests that the superior physical and chemical diversity of angiosperm hosts increases habitat heterogeneity, which in turn facilitates population divergence and sympatric speciation among associated insects (Futuyma & Agrawal 2009). Even the duration of this co-evolution remains debatable. There is an ever-growing discordance between the fossil record (still supporting an earliest Cretaceous angiosperm origin) and molecular dating estimates that now reject a post-Jurassic origin, some of which even suggest a latest Triassic origin (Doyle 2012; Barba-Montoya *et al.* 2018; Li *et al.* 2019).

At least, recent molecular phylogenies still support a mid-Cretaceous co-radiation of insects and angiosperms (Misof *et al.* 2014; Barba-Montoya *et al.* 2018; Li *et al.* 2019). However, this pattern remains challenged by an alternative hypothesis. A survey of insect evolutionary history revealed no significant increase in their taxic diversity at the family level (Labandeira & Sepkoski 1993; updated in Labandeira 2005, 2018). Using this approach, the middle of the Cretaceous would have had high origination rates, but also high extinction rates, with the disappearance of 31% of Early Cretaceous families (Ross *et al.* 2000; Labandeira 2005). This taxic approach results in the detection of two diversity maxima bracketing the period of angiosperm radiation (defined in this study as a 35-Myr interval spanning the Aptian to the Turonian), separated by a diversity minimum that may be driven by time-lag effects caused by the extirpation of most ancestral insect-gymnosperm associations and the slow acquisition of new insect-angiosperm associations (Labandeira 2014, Fig.13.3).

While studies based on taxic (usually family-level) diversity have the advantage of encompassing a wider range of orders among insects, they assume that all these families are

monophyletic and have equal diversity and ecological significance (Grimaldi & Engel 2005). Considering that some beetle families are more diverse than entire orders (Farrell 1998), and that the main ant and termite families have such a key role in modern ecosystems (Eggleton 2000; Wilson & Hölldobler 2005), the merits of these assumptions are highly debatable. Whether taxic, phylogenetic, or ecological/functional diversity is measured (Labandeira 2018), the Cenomanian seems to be the first age to witness an insect assemblage somewhat similar to that of the present.

While modern terrestrial ecosystems were established by the important plant and insect turnover in the middle of the Cretaceous, a smaller component of the insect biotic turnover occurred in fresh water. The Mesozoic Lacustrine Revolution profoundly changed lacustrine trophic networks from the Late Jurassic to the end of the Early Cretaceous (Buatois *et al.* 2016). It consists in a shift from detritivore dominated and very nutrient poor lakes (Zherikhin *et al.* 1998) to herbivore-dominated and slightly richer systems (Sinitshenkova 2002), which was completed by the Cenomanian. The extinction of 20 family and superfamily lineages was almost fully compensated (at this taxonomic level) by the origination of 19 new lineages (Buatois *et al.* 2016). Among Coleoptera, for instance, the extinction of iconic Jurassic and Early Cretaceous families such as Schizophoridae and Coptoclavidae was approximately synchronous with the appearance of the extant family Haliplidae (Buatois *et al.* 2016).

The middle of the Cretaceous seems a key milestone for the evolution of many eusocial insect lineages that have a disproportionately high influence on modern terrestrial ecosystems. This time records the oldest occurrences of bees, in Burmese and New Jersey amber (Michener & Grimaldi 1988; Poinar & Danforth 2006). The evolution of Formicidae in particular is the most consequential event in Mesozoic insect evolution altogether, with the oldest representatives of that family recorded in French and Burmese amber (Engel & Grimaldi 2005). These two amber deposits have produced queen and worker morphs of the same stem-group ant species, which demonstrates that some of the oldest known ants were already socially advanced (Perrichot *et al.* 2008a, b; Barden & Grimaldi 2016). In contrast, Haidomyrmecines are one of the stem lineages that do not show any character indicative of eusociality but show extreme morphogenesis with a concave frontal area and elongated ‘trap-jawed’ mandibles that may have had a predatory function (Barden & Grimaldi 2012; Perrichot *et al.* 2016). The most diverse Cretaceous ant fauna, mostly stem-group species from Burmese amber (19 species as of 2016), would have occupied a proportionally larger morphospace than that of modern crown-group ants (defined as having an

elongated scape along the antenna) (Barden & Grimaldi 2013, 2014, 2016). This suggests a rapid morphological diversification soon after the origin of Formicidae, which may have been no earlier than late Albian-Cenomanian due to their sustained absence from well sampled older lagerstätten (LaPolla *et al.* 2013). The oldest known crown ants are not much younger (Turonian), and are known from New Jersey amber (Grimaldi & Agosti 2000) and Orapa, Botswana (Dlussky *et al.* 2004). Formicidae are yet another insect taxon that may have diversified in concert with the angiosperm radiation: angiosperm forest leaf litter has been suggested as a center of origin for the entire family since it is the habitat with the highest ant abundance and diversity today (Wilson & Hölldobler 2005; Moreau *et al.* 2006). Extant Formicinae constitute a ludicrously high proportion of the biomass of modern tropical forests, yet a sparse amber record throughout the Cretaceous suggests that the family only reached ecological dominance after the extinction of stem ant lineages at the end of the period (Wilson & Hölldobler 2005; LaPolla *et al.* 2013).

Together, the angiosperm radiation and the Mesozoic Lacustrine Revolution are probably the main factors of the most recent episode of major insect faunal turnover (Labandeira & Sepkoski 1993). Their effects can be traced on a global scale, as opposed to the Cretaceous-Palaeogene (K-Pg) extinction event, where responses to this short-term crisis seemed to vary on a more regional scale (Labandeira *et al.* 2002; Wappler *et al.* 2009; Wing *et al.* 2009). The 10⁷-year duration of this terrestrial turnover may forever classify it in the realm of background extinctions, which may also explain the reluctance to adopt the phytocentric division of geological time between the fern and gymnosperm dominated Mesophytic and the angiosperm dominated Cenophytic (Wing & Sues 1992; Zherikhin 2002). Yet, it can be argued that this biotic turnover has affected the evolution of terrestrial ecosystems at a more fundamental level than any tetrapod turnover that occurred during the K-Pg mass extinction event.

1.2.5 Conclusions

The study of environmental trends in Cenomanian terrestrial ecosystems presents an interesting paradox. While almost all of the angiosperm macrofloras that can be used as robust quantitative palaeoclimate proxies are found at middle to high latitudes, the known diversity for almost every other terrestrial taxon is concentrated in select localities at low latitudes, most of which come from a few amber sites in northern Myanmar. The Cenomanian is one of these hothouse time intervals that display a very equable climate across a latitudinal gradient, which

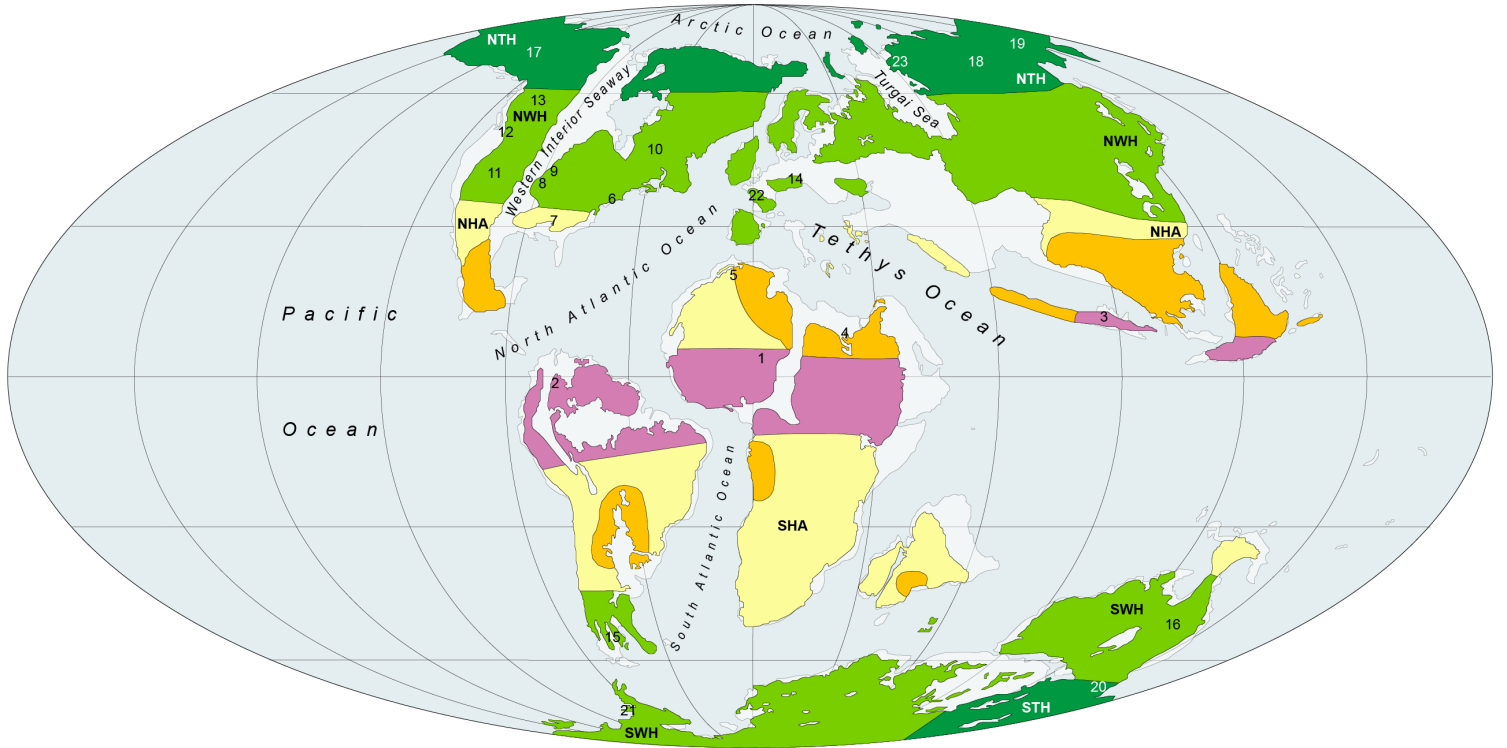
would make it a very interesting case study for testing hypotheses of latitudinal biodiversity gradients. The present diversity gradient is often explained by a high climatic disparity from the equator to the poles, with tropical ecosystems having far higher species richness (Fischer 1960). Multiple mechanisms have been proposed to explain the underlying role of climate (Mittelbach *et al.* 2007): ecological hypotheses usually cite the higher niche availability and carrying capacity of tropical ecosystems, while evolutionary hypotheses cite higher diversification rates in the tropics, as well as the older age of some tropical ecosystems implying more time for diversification.

Ample palaeontological data has already contributed to this debate, notably demonstrating higher origination rates in the tropics while offering mixed evidence for latitudinal differences in extinction rates (Jablonski *et al.* 2006; Mittelbach *et al.* 2007; Valentine *et al.* 2008). However, the Cenomanian fossil record has yet to provide a significant contribution compared with other hothouse periods such as the Palaeocene and early Eocene, in part due to the very unequal fossil record of this age. Yet the peculiar arrangement of vegetation zones for this age, where equatorial forests are rare and temperate forests extend to the poles, raises interesting questions. To what extent would the Cenomanian latitudinal diversity gradient be shallower than today? Would the correlation between latitude and diversity remain negative at all? The high plant diversity observed in polar and subpolar regions, most elegantly demonstrated in Russia and Alaska, definitely seems to point towards a shallower gradient. However, this hypothesis can only be further tested by an improved sampling effort at lower latitudes. This would also lead to a better understanding of relationships between atmospheric composition, fire intensity, and plant-insect interactions that may all have driven the diversification of the most dominant plant and animal groups of our modern ecosystems.

The discovery of more sites could also shed insight on possible causes for the exceptionally high biodiversity in Burmese amber: is it indeed representative of a widespread Cenomanian trend, or an exceptional case of endemism, or simply taphonomical bias? The skew in diversity caused by the exponential discovery rate from Burmese amber should only increase unless more fossil assemblages of similar age are discovered, whether they come from equatorial, tropical, temperate or polar latitudes. Until then, the power of studies of environmental trends in the middle of the Cretaceous on the influence of biotic and abiotic drivers of evolution in deep time will remain limited.

1.3 Figures

Figure 1. Palaeogeographic map of the world in the Cenomanian age (100.5 – 93.9 Ma). Palaeocontinent positions modeled after Scotese (2001). Climatic and vegetation zones are as follows: –Temperate Humid (dark green, Northern and Southern); Warm Humid (pale green, Northern and Southern); Hot Arid (yellow, Northern and Southern); Evaporite belts (orange); Equatorial Humid (purple); modeled after Chumakov *et al.* (1995) Localities cited in Chapter 1 are as follows: 1 – Echkar Formation, Niger; 2 – Une Formation, Colombia; 3 – Kachin amber, Myanmar; 4 – Bahariya oasis, Egypt; 5 – Kem Kem beds, Morocco; 6 – Raritan Formation and Amboy Clays (Potomac Group), USA; 7 – Tuscaloosa Formation, USA; 8 – Fort Harker, Dakota Formation, USA; 9 – Rose Creek, Dakota Formation, USA; 10 – Redmond Formation, Canada; 11 – Soap Wash flora, USA; 12 – Winthrop Formation, USA; 13 – Dunvegan flora, Canada; 14 – Peruc flora, Czech Republic; 15 – Mata Amarilla Formation, Argentina; 16 – Winton Formation, Australia; 17 – Nanushuk Group, Alaska, USA; 18 – Timerdyakh Formation, Vilui basin, Russia; 19 – Grebenka flora, Russia; 20 – Matakaea Group, New Zealand; 21 – Alexander Island, Antarctica; 22 – Charentes and Anjou amber, France; 23 – Taimyr amber, Russia.



BRIDGING TEXT

Eastern Canada is one of those regions of the world that have a very poor Mesozoic record, likely because of prolonged glacial erosion on the Canadian Shield. The only two localities of definite Cretaceous age are the Albian Mattagami Formation from northern Ontario (White *et al.* 2000) and the Cenomanian Redmond Formation, limited to an out-of-context lacustrine lens near the Quebec-Labrador border (Blais 1959; Dorf 1959).

The Redmond no.1 iron mine is located 16 km south-southeast of Schefferville (Dorf 1967) at a latitude of 54.7°N and a longitude of 66.7°W, which places it approximately 500 km north of the permafrost limit in the Quebec-Labrador Peninsula. As a result, the region is in the taiga subzone of the Quebec boreal vegetation zone, more precisely in the bioclimatic domain dominated by a black spruce-lichen forest (Ministère des ressources naturelles, 2016). Of the 36 plant species initially identified, 27 were angiosperms, and most of these were represented by medium-sized leaves that could have belonged to large trees that tolerate much milder climate conditions (Blais 1959; Dorf 1959). Many known fossil floras already showed that the Cretaceous was a globally warmer period than today, but this discovery provided the first relative palaeoclimate estimate for that period in the Quebec-Labrador Peninsula.

The following chapter addresses the first specific objective of this thesis by describing an updated analysis of the prevalent climate in Cenomanian Quebec/Labrador based on the Redmond flora. This is the first palaeoclimatic reconstruction for this locality to use a multivariate quantitative method, providing estimates of various temperature and precipitation parameters as well as length of the growing season. It also relies on a larger dataset, since the most recent excursions to the mine have increased the morphological leaf diversity known from this assemblage.

CHAPTER 2. Palaeoclimatic reconstruction for a Cenomanian-aged angiosperm flora near Schefferville, Labrador

Abstract

An understanding of local and regional climate trends is essential to investigate the remarkable angiosperm radiation that happened during the Albian-Cenomanian transition. However, many of the inland depositional environments pioneered by the first modern angiosperms are poorly represented in the fossil record. Eastern Canada in particular has a very poor Mesozoic record. In this paper, we present the first multivariate palaeoclimate analysis (CLAMP) for the environment of a geologically isolated woody dicot dominated flora found in the Redmond no.1 mine, Labrador, near Schefferville, with an estimated Cenomanian age. It reveals that the Redmond flora would have experienced a mean annual temperature of 15.1 ± 2.1 °C, one of the coolest recorded for North America at this time. These results confer the Redmond no.1 site a warm temperate and fully humid climate with a hot summer, in accordance with previous qualitative palaeoclimate estimates. This flora fits smoothly into palaeolatitudinal MAT gradients that use other Cenomanian-estimated North American floras. Despite an inland setting, the climate analysis does not recover a significantly higher degree of seasonality than the sites to which it is compared, which agrees with established climate equability models for the Cretaceous and Palaeogene. This study also introduces 15 new morphotypes discovered in recent fieldwork. The eventual description of the species they represent may refine our dating estimates for the Redmond Formation. A greater understanding of the depositional environment and of the natural history of these angiosperms is required to improve this community's characterization, along with estimates from other proxies.

2.1 Introduction

The Albian-Cenomanian transition in the middle of the Cretaceous period witnessed ecological and evolutionary changes that laid the foundations of modern terrestrial communities. Not least of these is the radiation of the angiosperms from the disturbed or early successional settings that had witnessed their evolution for the previous 30 Myr (Doyle & Hickey 1976; Crane *et al.* 1995). After thriving as lowland riparian and estuarine weeds (Royer *et al.* 2010), early

angiosperms underwent a spectacular ecological diversification and expanded their geographical range into more stable inland environments, often coinciding with the decline of established groups such as conifers, pteridophytes, ginkgoaleans and Bennettiales (Retallack & Dilcher 1986; Lupia *et al.* 2000; Coiffard *et al.* 2012).

Many of the hypotheses that attempt to explain this floral turnover revolve around a combination of biotic and abiotic factors. In certain modern environments, angiosperms are known to have a higher competitive ability than other plants due to higher productivity under high nutrient concentrations (Berendse & Scheffer 2009). This competitive ability may have led to positive feedbacks with increased fire regimes during the Albian-Cenomanian transition as global atmospheric pCO₂ and temperatures increased (Bond & Scott 2010). These abiotic changes may also have induced a positive feedback with photosynthetic capacity through an increase in venation complexity, which is correlated with an increase in wood hydraulic efficiency and the appearance of the first angiosperm trees (Philippe *et al.* 2008; Feild *et al.* 2011). This remarkable radiation can be explained in part by co-evolution with pollinating insects such as Hymenoptera and Lepidoptera (Grimaldi 1999; Labandeira 2014), but also by an understanding of global and regional climatic trends. The latter can be detected in the foliar physiognomy.

Despite a constant flow of newly described palaeofloras from across the world, some regions, such as eastern Canada, remain poorly represented in the fossil record. The southern half of the palaeocontinent of Appalachia is well represented by coastal and estuarine floras ranging in time from the Barremian to the Cenomanian (Newberry & Hollick 1886; MacNeal 1958; Doyle & Hickey 1976), and changes from the Albian to the Turonian are represented by floras from the western coast of Laramidia (Miller *et al.* 2006; Jonsson & Hebda 2015). In comparison, very little is known of Appalachia's northern inland ecosystems. Early palaeolatitudinal climate gradients established for Cenomanian North America were almost totally restricted to low palaeolatitudes around 30°N (Wolfe & Upchurch 1987), though updated gradients are complemented by recently studied floras from Alaska (Spicer & Herman 2010).

An enigmatic angiosperm-dominated flora from Labrador may provide insight into this poorly studied part of the Cretaceous world. Soon after its discovery alongside a few insect impression fossils during iron ore prospection near Schefferville, it was biostratigraphically correlated with North American Cenomanian-aged floras, though no detailed description was ever published (Dorf 1959, 1967). So far, no other Mesozoic angiosperm floras have been reported

from eastern Canada. This would also make it one of the earliest known woody dicot floras to flourish far inland, alongside assemblages from central Alaska's Yukon-Koyukuk basin (Herman *et al.* 2016), Siberia's Vilui basin (Spicer *et al.* 2008), and the Winton Formation of central-western Queensland (Fletcher *et al.* 2014). A quantitative palaeoclimate estimate using leaf margin analysis (LMA) has already been obtained for the Labrador flora and was compared with coeval floras to the north and south (Armstrong 1993; Miller *et al.* 2006). However, this univariate method for palaeoclimatic reconstruction is fraught with limitations (Greenwood *et al.* 2004; Peppe *et al.* 2011; Li *et al.* 2016) and estimates from this site have been based on a limited dataset.

In this paper, we present the first palaeoclimatic reconstruction founded on the Climate Leaf Analysis Multivariate Program (CLAMP) (Wolfe 1993; Spicer 2006) for this locality. The morphological diversity of the flora under study has also been expanded by the recent discovery of new leaf morphotypes on the field. These results are integrated to data from approximately coeval Cenomanian North American floras and refine our understanding of climatic trends at this ecosystem's local scale and at a broader continental scale.

2.2 Geological setting of the Labrador Cretaceous flora

The angiosperm flora that is the object of this study is preserved in the Redmond Formation, a sedimentary unit named after the Redmond no.1 mine, located 16 km south-south-east of Schefferville (Dorf 1967) at a latitude of 54°41'N and a longitude of 66°45'W, close to the Quebec border (Fig. 1). This abandoned iron mine contains the only known exposure of the formation in a very complex geological setting. It contains clastic minerals constituting three distinct lithologies, although almost all fossils have been found in just one of these: a fine-grained, evenly banded ferruginous argillite with a very pronounced umber colour and a 60% red hematite content (Blais 1959). Before iron ore mining operations brought the formation out of stratigraphical context, it formed a very restricted bed not exceeding 1.5 m in thickness, traced for approximately 152 m (Blais 1959). This bed was lying in the upper section of a basin-shaped space 1524 m long, 508 m wide, and up to 183 m deep containing sterile argillite and iron-rich 'rubble ores', which was in turn overlain by a 3 – 5 m overburden of glacial deposits (Dorf 1967; Séguin 1971). The argillite in the thin bed has a finer grain size, a darker colour, and a much higher abundance of well-preserved fossils, than the surrounding sterile argillite.

Hypotheses concerning the depositional environment of these fossils have yet to be tested. The most widely accepted one proposes a shallow lacustrine setting based on very fine grain size, a very thin lamination, and well-preserved soft tissues such as leaf and wing venation in fossilized plants and insects (Blais 1959). These characteristics distinguish low-energy freshwater systems such as lakes from higher-energy fluvial/deltaic systems in which soft-bodied organisms are more likely to be decomposed (Behrensmeier and Hook 1992, pp.42-43). Blais (1959) stated that the high alumina content displayed in the argillite is indicative of a lateritic palaeosol, a soil type usually formed in tropical to subtropical climates (Craggs *et al.* 2012), although this evidence alone is barely sufficient to suggest a hypothesis. Historical fossil collections for the site contain angiosperm leaves representing at least 27 species, which are the main focus of this study, along with at least one lycopod, at least four true fern species (spread among Polypodiales and Gleicheniales), and at least four conifer species (Dorf 1959, 1967; Armstrong 1993; Fig. 2). Along with an assortment of insect species (Carpenter 1967; Emerson 1967; Ponomarenko 1969; Rice 1969; Fig. 3), these fossils offer a glimpse of a lakeshore environment surrounded by an angiosperm-dominated mixed mesophytic forest.

The Redmond basin is underlain unconformably by stratified iron ores found in jaspoid and carbonate-silicate cherts that are part of the iron-rich Sokoman Formation, deposited around 1878 Ma in the Palaeoproterozoic (Conliffe 2016). The Sokoman is underlain by the Ruth Formation, composed of ferruginous shale (Blais 1959). Together, they are part of the Kaniapiskau Supergroup, the geological unit that constitutes the Labrador Trough, a 48 km wide folded and faulted geosyncline containing sedimentary and volcanic rocks that stretches for approximately 1120 km along the border of northeastern Quebec and western Labrador (Zajac 1974; Conliffe 2016), and along the eastern margin of the Archaean Superior Province (Conliffe *et al.* 2012).

The Labrador Trough was formed by two main orogenic events : a period of folding in the late Precambrian (between 1500 and 1250 Ma), and a later one for much of the Mesozoic that probably led to the opening of the North Atlantic ocean between 250 and 200 Ma (Tremblay *et al.* 2013; Conliffe 2016). The Redmond basin is likely the remnant of a graben: this folding and down-faulting continued after the deposition of the Redmond fossiliferous argillite bed resulting in its steep dip of 45° to the east (Blais 1959). As this tectonic activity increased the graben's depth, it was progressively infilled with muddy sediments containing dead leaves and insects (in the case of the Redmond Formation), and/or rubble ores of clastic origin mixed with fallen trees. Similar

basins were reported in the French, Burnt Creek and Ruth Lake mines, located 4 km west of Schefferville. In Ruth Lake, entire lignitized tree stumps were found in a breccia 30 m below ground surface, some of which reach almost 1 m in diameter (Usher 1953). They are now also out of context because of the mining activity that followed their discovery.

The presence of a megafloral assemblage in the ferruginous argillite bed provides the only relative dating estimate for the Redmond Formation itself. Dorf (1959) conducted a biostratigraphical correlation with already known North American floras and found that it was most similar in composition to the Raritan, Dakota, and Tuscaloosa formations, which are all considered to be of Cenomanian age, between 93.9 and 100.5 Ma (Cohen et al. 2018; Fig. 1).

Based on the interbedding between the clays and the rubble ores, Blais (1959) concluded that the latter must have been of similar age (Late Cretaceous) and included them in the Redmond Formation. Assuming its dating is correct, this makes it the only known exposure from the Mesozoic era in the Quebec/Labrador Peninsula. The sedimentary unit in closest spatial and temporal proximity would be northern Ontario's Albian Mattagami Formation (White *et al.* 2000).

While the age of the argillite formation is already poorly constrained, that of the surrounding rubble ores is even more debatable. The interbedding noted by Blais (1959) only proves that some of the leaching happened during the Cretaceous (Conliffe *et al.* 2012; Conliffe 2016). The implied long duration of fault movement and resulting rubble ore formation restrains us from including the entirety of the region's rubble ores in the Redmond Formation (*contra* Blais, 1959). This makes it impossible to correlate the Ruth Lake wood to the insects and leaves found in the Redmond no.1 mine's ferruginous argillite, and so renders the tree stumps' cell structure unsuitable as an alternative palaeoclimate proxy (Carlquist 1977; Wolfe & Upchurch 1987) for Cenomanian eastern Canada.

2.3 Material and method

2.3.1 Fossil collection and identification

The fossils used in this study were collected from the Redmond no.1 mine over five separate occasions: the first in September 1958 for Princeton University (Dorf 1959; Rice 1969), which now resides at the Yale Peabody Museum of Natural History (YPM); two for the Geological Survey of Canada (GSC) (G. Gross, 1960 and D.C. McGregor, 1961); one in 2013 by the *Musée de paléontologie et de l'évolution* (MPE); and a joint expedition between the MPE and the Redpath

Museum (RM) in August 2018, in which the first author participated. On the 2013 and 2018 expeditions, the fossils were surface collected from spoil piles scattered around the now flooded mine since the original bed had long been destroyed by mining activities. Alongside new leaf specimens, new insects were discovered, including the first aquatic nymphs reported from the site, as well as more complete aquatic coleopteran specimens (Figs 3A, 3C; AVD-P & HCEL, in prep.). The 2013 expedition also produced ichnofossils of bioturbators moving along the water bottom (Fig. 3F). A survey of neighbouring mines in 2018 did not reveal any exposed fossil-bearing argillites similar to those found in the Redmond no.1 mine.

The YPM collection is the only one in which an attempt to identify the flora was made before this study. Its classification was undertaken by Leo J. Hickey; the notes he left with the YPM specimens were consulted by the first author to guide our subsequent identifications. A total of 177 specimens have been assigned to 46 morphotypes using leaf architectural characters (Hickey 1973; Ellis *et al.* 2009). The identification of most of the morphotypes in this study agrees with the species identifications originally performed by Hickey. However, 15 morphotypes are based on new leaf forms discovered in the 2013 and 2018 expeditions, and one is based on a specimen observed at the GSC (Demers-Potvin & Larsson 2019). Each has been assigned a morphotype quality index (MQI), ranging from 0 to 7, that expresses the completeness of the specimens on which it is founded (for details see Harris & Arens 2016). The argillite tends to fracture conchoidally, which means that leaves found along bedding planes are often fragmentary. The ensuing loss of morphological characters introduces much uncertainty in the attribution of a specimen to a given morphotype. For this reason, many of the leaf fragments collected could not be integrated into the analysis.

A summary of the morphotypes is presented in Table 1. Photographs of the morphotype exemplars are presented in Figs 4 – 7. GSC, MPE and RM specimens were photographed with a Sony a6000 camera with an FE2.8/50 macro lens, and YPM specimens with a Nikon D7100 camera with a 50mm macro lens. Measurements used in the descriptions were made on Fiji (Schindelin *et al.* 2012). More complete descriptions are found in Demers-Potvin & Larsson (2019).

2.3.2 *Palaeoclimatic Reconstruction*

One way of estimating a palaeoecosystem's climate using biological proxies is to infer it from the physiognomy of its fossil leaves. A positive correlation in many extant floras between the percentage of species with untoothed margins and their habitat's mean annual temperature (MAT) was first proposed by Bailey & Sinnott (1915, 1916), and later became the basis for the univariate method of leaf margin analysis (LMA) (Wolfe 1979; Wing & Greenwood 1993; Wilf 1997; Greenwood 2007). Based on the observation that leaf physiognomy responds to multiple environmental factors (Dolph & Dilcher 1979), a more complex palaeoclimate reconstruction model, the Climate Leaf Analysis Multivariate Program (CLAMP), was developed by Wolfe (1993) and subsequently refined (*e.g.* Spicer 2006; Yang *et al.* 2015). This is the first time that the Redmond flora's climate has been estimated with this method. Every CLAMP analysis on a fossil assemblage is based on two spatially related modern datasets. The first is a physiognomic calibration dataset composed of extant floras from sites worldwide that have been scored for the same character states as fossil sites. Every physiognomic calibration dataset has its corresponding meteorological calibration dataset in which, in the most common configuration, 11 climate parameters found to be correlated with leaf physiognomy have been measured on each site or derived from standard global gridded data. The data from physiognomic and meteorological dataset matrices is united in a canonical correspondence analysis (CCA) (ter Braak 1986). The morphotypes of a given fossil site are then scored using the same protocol as the modern sites. This positions a fossil leaf assemblage passively in the physiognomic space formed by leaves from extant calibration vegetation, leading to quantitative predictions of palaeoclimate parameters at the time of fossil deposition. Further details on the method can be found on the CLAMP website (Spicer 2006; Yang *et al.* 2011, 2015).

To ensure a sufficiently high statistical precision for the results, a minimum of 20 fossil morphotypes (Wolfe 1993), with a scoring completeness greater than 66% (Yang *et al.* 2011), is recommended. After its 46 morphotypes were scored, the Redmond flora displayed a CLAMP scoring completeness of 65% (see scoresheet in Demers-Potvin & Larsson 2019). The matrix was analyzed using the CLAMP Online tool (Spicer 2006; Yang *et al.* 2011). A preliminary CLAMP analysis was made using global calibration files (PhysgGlobal378 and HiResGRIDMetGlobal378, $n = 378$ sites), which positioned the Redmond flora well away from sites in cold climates (Spicer 2006). Extraneous evidence of an environment that did not experience a freezing period comes

from the occurrence of an entomofauna in which some taxa are predominantly associated with tropical to subtropical climates, such as a medium-sized phasmatodean (Rice 1969; Brock 2004: 222; Fig. 3B), a termite (Emerson 1967; Grimaldi and Engel 2005; Fig. 3D), and a snakefly belonging to the extinct family Alloraphidiidae (Carpenter 1967; Grimaldi and Engel 2005; Fig. 3E).

A more definitive analysis was performed using the Physg3brcAZ calibration dataset derived from temperate Northern Hemisphere sites ($n = 144$). Climate calibrations were made using both the gridded (GRIDMet3brAZ) and ungridded (Met3brAZ) meteorological datasets to compare results between the two sampling methods. While the ungridded dataset is based on calibration vegetation sites, the gridded dataset attempts to correct for the lack of climate stations close to potential calibration vegetation sites at low latitudes by using a $0.5^\circ \times 0.5^\circ$ grid of global interpolated climate data based on the dataset of New *et al.* (1999) (Spicer *et al.* 2009).

2.4 Results

The CLAMP results for the Redmond no.1 site are presented in Table 2. The first CLAMP analysis for this locality presents a MAT of 15.1 ± 2.1 °C. The results from gridded and ungridded datasets are statistically indistinguishable, in accordance with Spicer *et al.*'s (2009) tests.

Not only does the palaeoclimate data from the Redmond flora yield invaluable information on the environment of a region otherwise devoid of Cretaceous fossils, but the site would have occupied a palaeolatitude estimated at 48.8°N (Van Hinsbergen *et al.* 2015a; Table 3). This means it is the most northerly site from eastern North America to present an early Late Cretaceous angiosperm flora, since the age of Greenland's Atane Formation is questionable (Wolfe & Upchurch 1987; Boyd 1993). This palaeolatitude is poorly represented in the eastern North American Cenomanian angiosperm fossil record (Miller *et al.* 2006). The climate parameter values of the Redmond no.1 site were then compared with coeval North American Cenomanian floras (Table 3). Comparative mean annual temperature values from leaf-margin analysis (LMAT) were obtained from entire-margin frequencies of 12 sites compiled by Miller *et al.* (2006). The original LMAT estimates for the Redmond Formation were calculated by Hickey & Armstrong (1998), those for the Raritan, Patapsco, Dakota, Woodbine and Dunvegan formations were calculated by Wolfe and Upchurch (1987), and that of Chandler, Alaska, was calculated by Parrish and Spicer (1988).

Comparative CLAMP values were obtained from GRIDMET3BR analyses of three sites: Tuscaloosa, Woodbine (Spicer & Herman 2010), and Nanushuk (Herman *et al.* 2016). Additionally, two floras from the Dakota Formation (age Cenomanian) were scored for CLAMP estimates (see Methods) to increase the Cenomanian site sample size. One of these floras was collected in Fort Harker, Ellsworth County, Kansas, during separate expeditions (Lesquereux 1892), and is now curated at the Yale Peabody Museum of Natural History (YPM). After examination, it was divided into 92 morphotypes with 89% completeness. The other, found in Rose Creek, Jefferson County, Nebraska, was scored from published descriptions (Upchurch & Dilcher 1990) into 18 morphotypes with 68% completeness. The CLAMP scoresheets for these additional floras are provided in Demers-Potvin and Larsson (2019).

The MAT data from Table 3 was then plotted against palaeolatitude with separate regressions for the LMA and CLAMP estimates on Fig. 8. For each site, palaeolatitude estimates were obtained from Van Hinsbergen *et al.* (2015a), using the reference frame of Torsvik *et al.* (2012) (see Van Hinsbergen *et al.* (2015b) for more details). We still deem the LMA-based implied regression a necessary comparison because it is based on a larger sample size than the CLAMP-based regression. The R^2 values and regression equations are presented in the caption to Fig. 8.

2.5 Discussion

The dominance of medium-sized angiosperm leaves in the Redmond assemblage, as well as the presence of insect taxa accustomed to mild or warm climates, led to qualitative hypotheses predicting a warm temperate to subtropical climate (Blais 1959; Dorf 1959). According to the updated Köppen-Geiger climate classification system (Kottek *et al.* 2006), the region's coldest month mean temperature (CMMT) of $7.8 \pm 3.4^\circ\text{C}$ is between the -3°C and 18°C values that define warm temperate climates, its disparity in precipitation between the three wettest and three driest months is nonsignificant, and its warm month mean temperature (WMMT) exceeded 22°C . A marked disparity of more than 15°C between CMMT and WMMT, along with a growing season of 8.4 ± 1.1 months, is indicative of a moderate seasonality. The growing season would have been far longer than that of more extreme environments such as Late Cretaceous Alaska's polar deciduous forests (Herman *et al.* 2016), which is not surprising considering the Redmond Formation's intermediate palaeolatitude and coincidentally long photoperiod. These quantitative results confer the Redmond no.1 site a warm temperate and fully humid climate with a hot summer

(Cfa) (Kottek *et al.* 2006), which confirms the initial qualitative hypotheses. This precision in climate classification was attained in part because of the multivariate nature of CLAMP.

Contrary to the LMA used in previous work on the Redmond Formation (Armstrong 1993; Hickey & Armstrong 1998), CLAMP encompasses 12 more leaf physiognomic characters that demonstrate a response to climate parameters. These additional variables provide more insight into an extinct ecosystem's seasonal cycle and photoperiod (Herman *et al.* 2016). By acknowledging the covariation between many leaf traits and multiple environmental factors (Dolph & Dilcher 1979), CLAMP assumes that a climate signal can be obtained from more correlations than the single correlation on which LMA is founded (Wolfe 1993; Spicer 2006; Yang *et al.* 2015). Conversely, leaf margin analyses of floras found in freshwater settings (the most common depositional environment) are more susceptible to confounding factors such as soil hydrology (Kowalski & Dilcher 2003), overrepresentation of toothed-margined species in riparian settings (Burnham *et al.* 2001) and evolutionary history (Greenwood *et al.* 2004; Little *et al.* 2010; Peppe *et al.* 2011). CLAMP also has an advantage over climate analysis methods based on more continuous leaf character states, such as digital leaf physiognomy (Royer *et al.* 2005; Greenwood 2007; Peppe *et al.* 2011), since it has been thoroughly tested for a longer time, and its uncertainties better addressed and understood (Wolfe 1993; Spicer 2006; Yang *et al.* 2015). Despite the fact that a single character (leaf margin) still explains >80% of the variance in MAT (Wing & Greenwood 1993; Wilf 1997), the CLAMP results from the gridded dataset remain the most accurate ever produced for the Redmond flora.

2.5.1 *Sampling uncertainties*

The completeness score of the Redmond flora is just below the recommended threshold of 66%, so information loss for some characters may affect the results. The fragmentary nature of many of the new morphotypes (often represented by only one RM specimen) takes a particular toll on the completeness of the dataset. When they are removed, it rises to 80%. Unsurprisingly, the morphotypes with the highest sample size (8 and 26) are also those that display the highest phenotypic plasticity (Figs. 4G, I - K, 6D - F; Demers-Potvin & Larsson 2019). Conversely, the small sample size of most morphotypes (91.3% represented by fewer than 10 specimens; see Table 1) means that much of the phenotypic plasticity characteristic of Cenomanian floras is not detected in the fossil assemblage (Spicer, pers. comm., 2019), which may lead to over-splitting of

morphotypes in the presence of newly acquired specimens with new morphological character combinations. It has been demonstrated that incomplete preservation has a particularly detrimental effect on the accuracy of palaeoclimate estimates derived from sites with many singletons (Royer *et al.* 2005), as is the case for the Redmond flora (Table 1). At least, the high number of singletons leads to a morphotype diversity that is much higher than the recommended minimum (see Material and Method, above). Demers-Potvin and Larsson (2019) discuss the erection of these new morphotypes, but a more detailed description of potentially new species is necessary to resolve their status.

Another sampling uncertainty has biological ramifications for the climate predictions. It is assumed in this study that all angiosperm leaves recovered are indeed woody dicots (Dorf 1959, 1967). Hickey and Armstrong (1993) classified YPM specimens of very small size in this guild, and so the classification of morphotypes discovered in more recent expeditions maintained this consistency. It has been shown that herbaceous plants display much less consistent physiognomic responses to climate (Li *et al.* 2016), but their effect on our results are probably trivial, because their leaves do not shed, and so rarely fossilize. In turn, this statement assumes that Late Cretaceous lacustrine palaeofloras are sufficiently similar to modern ones.

In any case, the more taxon-dependent data supports the woody dicotyledonous nature of this flora. Table 1, Figs 4 – 7 and Demers-Potvin & Larsson (2019) show that many of these morphotypes can reach a notophyll size class and a complex venation pattern, which are characteristic of woody dicots. Many are comparable in size and complexity to newly discovered leaves from the Turonian Mancos Shale Formation which have been attributed to trees (Jud *et al.* 2018). This would make the Redmond flora slightly older, assuming the relative dating of the formation is accurate (see Geological Setting, above).

Taxon-independent leaf economic traits could also be determined. One such trait is vein density (D_v), which has been shown to reflect life-form in angiosperm leaf assemblages (Crifò *et al.* 2014) and could be quantified on a much larger sample size. Leaves with a higher D_v have an improved photosynthetic capacity, and their synchronous appearance with the oldest angiosperm wood known suggests that it was a key adaptation to the increase in hydraulic capacity necessary to sustain such complex organisms as trees (Philippe *et al.* 2008; Feild *et al.* 2011). This study should be the next step to improve the ecological characterization of each species of the Redmond flora, refining our capacity to build subsequent CLAMP datasets. Most importantly, its results

could support Dorf's (1959, 1967) hypothesis that the larger Redmond leaves belong to some of the oldest known angiosperm trees.

2.5.2 *Local spatial and temporal resolution*

Blais' (1959) description of the Redmond Formation in geological context is highly valuable, since it is the only way for modern workers to gain insight into the site's geological setting. Furthermore, the hypothesis of a lacustrine depositional environment is now confirmed after the discovery of the first articulated and relatively complete specimens of aquatic insects (Figs 3A, C; AVD-P & HCEL, in prep.). The argillite's fine grain size and thin laminations were already indicative of a lake environment (Picard & High 1972), and so is the remarkable preservation state of some of the newly discovered insects (Grimaldi & Engel 2005).

However, Blais' survey did not address the site's temporal resolution since it did not approach it from a palaeoecological perspective. The formation's modest depth of 1.5 m (Blais 1959) and its lacustrine origin suggest a high temporal resolution (Behrensmeyer & Hook 1992). Unfortunately, Blais did not calculate sedimentation rates based on its laminations, nor did he map fossil occurrences along a stratigraphic section, to support his hypothesis. If such a section had been produced, it might have been possible to infer the lake's variations in oxygen content, which could have been inferred by mapping the occurrences of ichnofossils produced by benthic bioturbators (Behrensmeyer & Hook 1992). In turn, insight on oxygen content could have contributed to an explanation of the fauna and flora's preservation state. It is mentioned that the bed was evenly laminated, but it remains difficult to estimate the duration represented by each lamination in this argillite. As for the distribution of the flora along the temporal axis of the formation, it is not specified whether plants were concentrated at a few levels, or widespread along the entire stratigraphic column (Dorf 1967). This means that any palaeoclimate estimate derived from this flora must account for some taphonomic time-averaging. Further sedimentological analyses of these argillite laminations, as well as a refinement of the current relative dating estimate based on the description of new macrofossils and palynological analyses, may provide insight on this issue.

As for the spatial resolution, it is quite difficult to assess, since most of the leaves found in the fossil assemblage could have belonged to trees growing away from the lake's vicinity (Greenwood 1992). At least, the specimen that represents Morphotype 46 might be of a more

autochthonous origin (Fig. 6O; Demers-Potvin & Larsson 2019). This leaf displaying a peltate petiole origin is very similar to leaves from the Potomac Group that were proposed to be floating on the water surface, a substrate where there is less mechanical stress on the petiole (Hickey & Doyle 1977). On the other hand, a peltate petiole origin is also encountered in leaves growing from tropical forest trees (Jacques *et al.* 2015). Since its habitat is not certain and its morphotype quality is among the highest (Table 1), we have decided to include it in the CLAMP analysis along with other morphotypes whose woody dicotyledonous status is less equivocal.

2.5.3 *The Cenomanian Quebec/Labrador climate in a North American context*

The Redmond MAT is the coolest recorded for Albian-Cenomanian eastern North America, and likely attributable to the combination of a higher latitude than other known sites and an inland location. Such conditions have been reported elsewhere at this time (Spicer *et al.* 2008; Herman *et al.* 2016). Complementary CLAMP results suggest a moderate seasonality in the Redmond flora's inland setting (Table 3), though it certainly was not as high as Armstrong (1993) imagined: neither the length of the growing season (LGS) nor the disparity between CMMT and WMMT are significantly different from the other sites it was compared with. The MAT gradient suggests either a genuine climatic equability between inland and nearshore environments in Cenomanian eastern Canada, or locally mild riparian conditions favourable to angiosperm invasion, or both. Given the global warming that was occurring during the Albian-Cenomanian transition, the latter hypothesis must be considered (Arens & Harris 2015), although it can only be tested with the discovery of more exposures of the Redmond Formation in Quebec and Labrador. In any case, the probable woody dicot life-form of most morphotypes indicates that they could thrive in more stable environments alongside gymnosperms by the Cenomanian, which is consistent with the floral composition of approximately coeval assemblages (Spicer & Herman 2001; Spicer *et al.* 2002).

For the moment, it is more parsimonious to argue that the data agrees broadly with a trend of continental sites showing a much more equable seasonal range of temperatures in the Cretaceous and Palaeogene than in the present (Wing & Greenwood 1993; Spicer *et al.* 2008). In the Cretaceous, North America was rotated clockwise so that the western landmass of Laramidia was situated further north (Spicer & Herman 2010; Bamforth *et al.* 2014; Herman *et al.* 2016) and the eastern landmass of Appalachia (of which the Quebec/Labrador Peninsula constituted the northern

extremity) was situated further south. It is no surprise, then, that a site that had a lower palaeolatitude in the Cretaceous than today, coupled with a far more equable MAT gradient, had such a mild climate with a long photoperiod that supported such a luxuriant flora.

The gradient derived from Miller *et al.* (2006) using LMA has a markedly steeper slope than that derived from CLAMP (Fig. 8). In light of the previous discussion, the larger sampling biases associated with LMA seem to lead to a less equable climate gradient model. Not only do MAT estimates seem more accurate with CLAMP than with LMA at the local scale, but they seem more precise at the regional scale and provide additional information about seasonality and photoperiod.

2.5.4 *Limitations of regional to global palaeoclimate studies*

The Albian-Cenomanian transition is probably the earliest time in geological history to be suitable for palaeoclimate analyses based on CLAMP and LMA, since it witnesses the advent of the few angiosperm life-forms to show a relationship between leaf physiognomy and climate parameters (Lupia *et al.* 2000; Feild *et al.* 2011). No wonder it is accurate only for sites less than 100 myr old (Wolfe 1993; Spicer 2006). This implies that results for a flora that probably existed very close to this time limit must be interpreted with caution.

Since CLAMP assumes that the physiognomic response of leaves to climate has not significantly changed for 100 myr, it has been suggested that it is more difficult to apply it confidently to older assemblages (Peppe *et al.* 2011). This could be a particular problem for assemblages representing ecosystems without any modern analogue, such as the Cretaceous polar mixed deciduous forests of Alaska (Spicer & Herman 2010; Herman *et al.* 2016). Furthermore, Albian-Aptian species that have a similar morphology to Late Cretaceous woody dicotyledons (Hickey & Doyle 1977) were long considered too evolutionarily distant to have a similar physiognomic response to climate, despite evolving under the same physical and mechanical constraints as modern leaves. Since the Cenomanian was a time of rapid global warming, early woody dicots were thought to be largely experimental forms that could not be assumed to behave similarly to modern forms (Spicer & Parrish 1986). If the physiognomic response of Cenomanian leaves to climate displayed a strong phylogenetic signal, a better understanding of these species' evolutionary history could help alleviate the uncertainties in 'taxon-independent' methods such as CLAMP (Little *et al.* 2010). However, many genera from this time interval display phenotypic

plasticity, which could blur the phylogenetic signal. This phenomenon is observed in at least two of the Redmond flora's morphotypes (Figs. 4G, I - K, 6D - F; Demers-Potvin & Larsson 2019; Spicer, pers. comm., 2019).

Since this assumption was made, however, many more fossil assemblages have been scored with CLAMP, and none of the Albian-Cenomanian floras (including the Redmond flora) have plotted outside the modern calibration space to suggest a significant change in the climate-physiognomy relationship (e.g. Fletcher *et al.* 2014; Arens & Harris 2015). Furthermore, a global study of the 378 CLAMP sites has demonstrated that biogeographic history has little effect on the observed correlations between leaf form and climate (Yang *et al.* 2015). In light of these considerations, the validity of the Redmond flora for palaeoclimate estimates should be further assessed by a more formal taxonomic description of the new species present among the morphotypes recognized in this study.

This constraint leads to another, where Cenomanian angiosperm sites with a diversity of woody dicot morphotypes sufficient for CLAMP scoring are rare, as is the case in North America (Wolfe & Upchurch 1987; Miller *et al.* 2006). This inevitably leads to systematic time-averaging of different sites, for instance in the case of our palaeolatitudinal MAT gradient. Since the global climate in the Cenomanian was changing quite rapidly, and since many of the sites used (such as Redmond no.1) have a very poor stratigraphic control, a gradient for this age contains especially large uncertainties. In this regard, the discovery and scoring of new palaeofloras (Jud *et al.* 2018) remains an essential aspect of palaeoclimatology based on biological proxies.

2.6 Conclusions

This is the first palaeoclimate estimate for the environment of the Redmond flora to use a multivariate method (CLAMP). At the local scale, its results confirm previous hypotheses according to which 'early' Late Cretaceous Quebec/Labrador would have experienced a mesothermal humid climate with a hot summer and offer a small glimpse of an environment that, to our knowledge, has been very sparsely preserved in the fossil record. Together, they contribute significantly to our understanding of Cretaceous eastern Canada, in the hope of refining the testing of hypotheses on the angiosperms' remarkable radiation.

The CLAMP results support a general Cretaceous and Palaeogene trend of inland environments having a climate as equable as that of coastal environments. However, such

comparisons at the regional to global scale with sites from the same age bin with poor stratigraphic control must be treated cautiously, since they can lead to systematic time-averaging that confounds observed palaeolatitudinal climate trends. This is especially concerning for periods of rapid climate change such as the Albian-Cenomanian transition, and it leads us to favour the detection of such climate trends at a more local scale to gain more insight on the radiation of the angiosperms. We acknowledge that the Redmond Formation does not have an ideal geological setting to support palaeoecological investigations, which is regrettable considering the scientific importance of one of the oldest inland angiosperm floras known. The Labrador Trough must be prospected further in the hope that more of this mysterious palaeoecosystem can be revealed.

Beyond palaeoclimate estimates, this study also contributes to an expansion of the morphological angiosperm diversity from the Redmond no.1 site, with the addition of 16 new morphotypes. Their formal description is essential: a more complete flora (complemented by an eventual study of the palynoflora) refines biostratigraphical correlations to estimate its age, and some species may increase broad-leafed tree diversity in the fossil record at a time in which they were radiating. The ecological characterization of the community must also be refined, either by studying leaf economic traits such as leaf vein density to gain insight on many morphotypes' life-forms, or by increasing our understanding of this flora's depositional environment. In turn, this will define much more clearly the assemblage that can be tested in future palaeoclimate estimates based on biological proxies. An estimate from an alternative geochemical proxy, such as clay weathering, could also support the study that has been presented here.

2.7 References

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2.8 Figures

Figure 1. Situation of the Redmond Formation in geologic time and in space. **(A)** Geological timescale placing the Redmond Formation in the context of major Cretaceous environmental trends; absolute ages based on Cohen *et al.* (2018); timing of oceanic anoxic events from Ogg *et al.* (2004); relative diversity of major plant groups based on Butler *et al.* (2009). **(B)** Location of the Redmond Formation near Schefferville in Labrador ($54^{\circ}41'N$, $66^{\circ}45'W$); exposures of the Sokoman Formation based on Conliffe (2016).

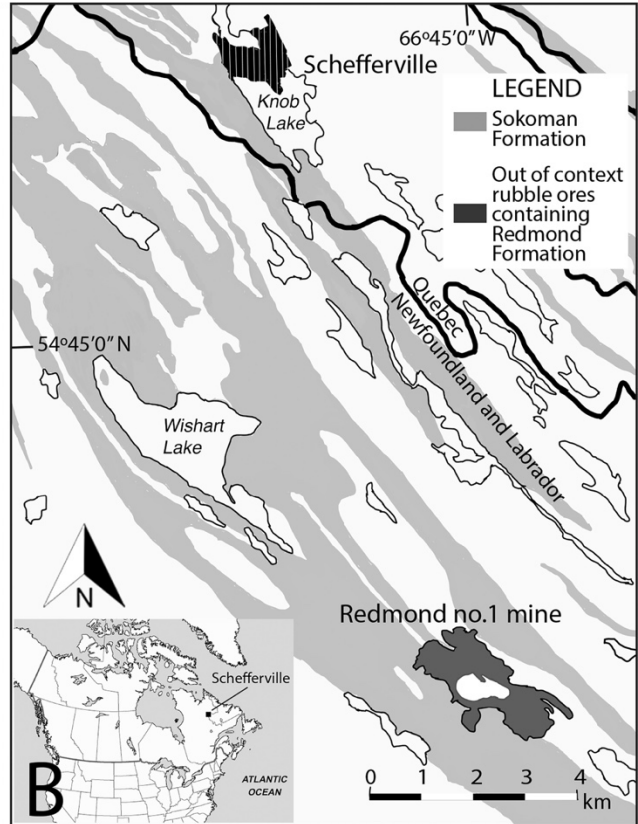
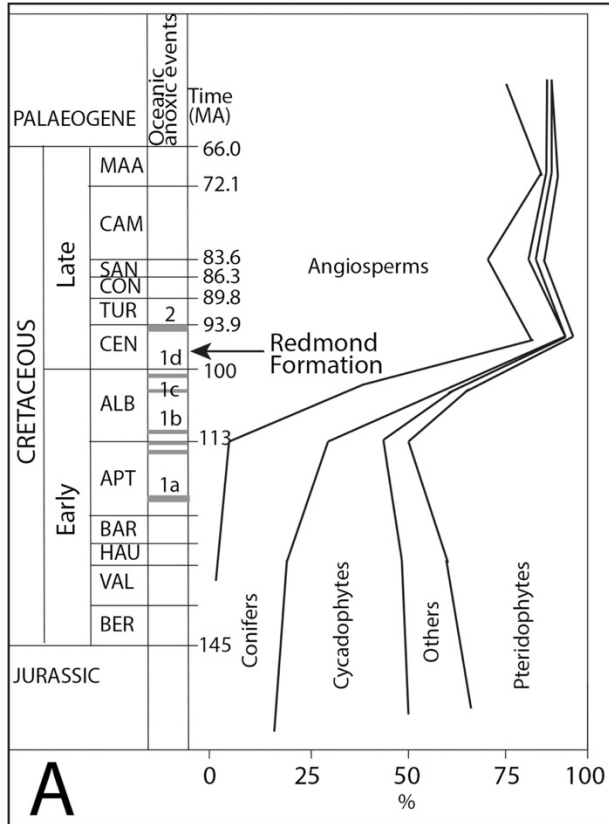


Figure 2. Some representatives of the non-angiosperm organisms preserved from the Redmond ecosystem. **(A)** Two young curled fern fronds (Gleicheniales), RMPB 2018.18.30. **(B)** Partial leaf of the cupressaceous conifer *Widdringtonites subtilis* Heer, YPM 30546. **(C)** Partial leaf of the pinaceous conifer *Abietites longifolius* (Fontaine) Berry, RMPB 2018.18.29. **(D)** Isolated fern frond attributed to *Asplenium angustipinnata* Fontaine (Polypodiales), YPM 30541. **(E)** Partial leaf of the cupressaceous conifer *Sequoia gracillima* (Lesquereux) Newberry, YPM 30529. Plants identified by Hickey (notes left alongside specimens). Scale bars 1 cm. Images adjusted for brightness and contrast.

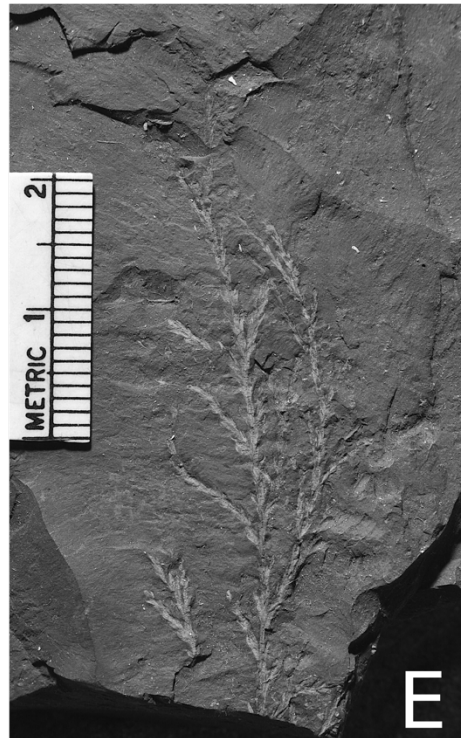
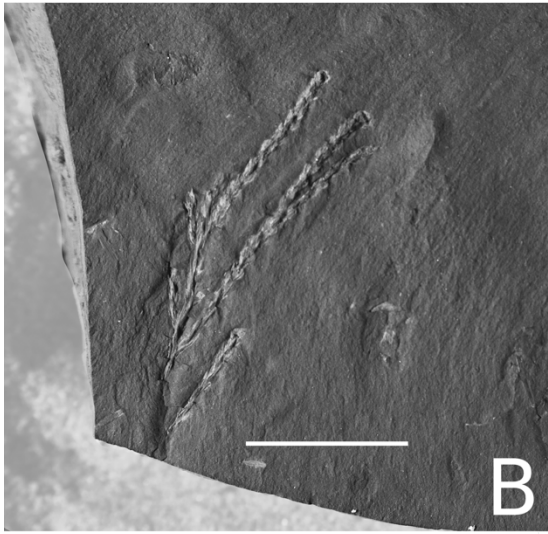
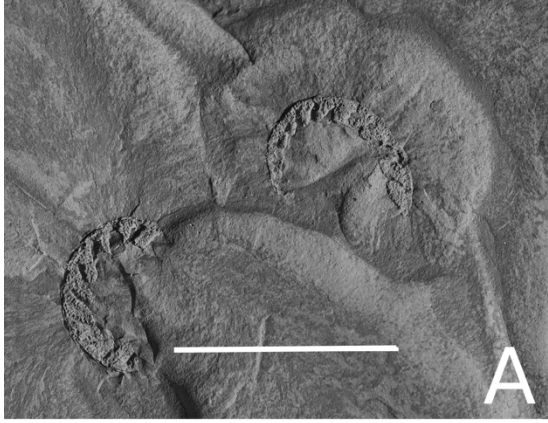


Figure 3. Some invertebrate remains indicative of the Redmond Formation's palaeoclimate and depositional environment. **(A)** Almost complete undescribed mayfly nymph (Ephemeroptera, Hexagenitidae), MPEP 1156.5. **(B)** Folded wings of large phasmatodean *Palaeopteron complexum* Rice 1969, GSC 22189. **(C)** Articulated scutellum and elytra of undescribed water beetle (Coleoptera, Adephaga, Hydradephaga), MPEP 702.4. **(D)** Isolated fore wing of termite (Hodotermitidae) *Cretatermes carpenteri* Emerson 1967, YPM 223802. **(E)** Isolated fore wing of snakefly (Alloraphidiidae) *Alloraphidia dorfi* Carpenter 1967, YPM 223803. **(F)** Ichnofossil of unknown burrowing benthic invertebrate, MPEP 702.41. **A, C** and **F** represent autochthonous remains from a lacustrine depositional environment; **B, D** and **E** represent allochthonous remains indicative of a warm palaeoclimate. Scale bars 5mm or marked in mm. Images adjusted for brightness and contrast.

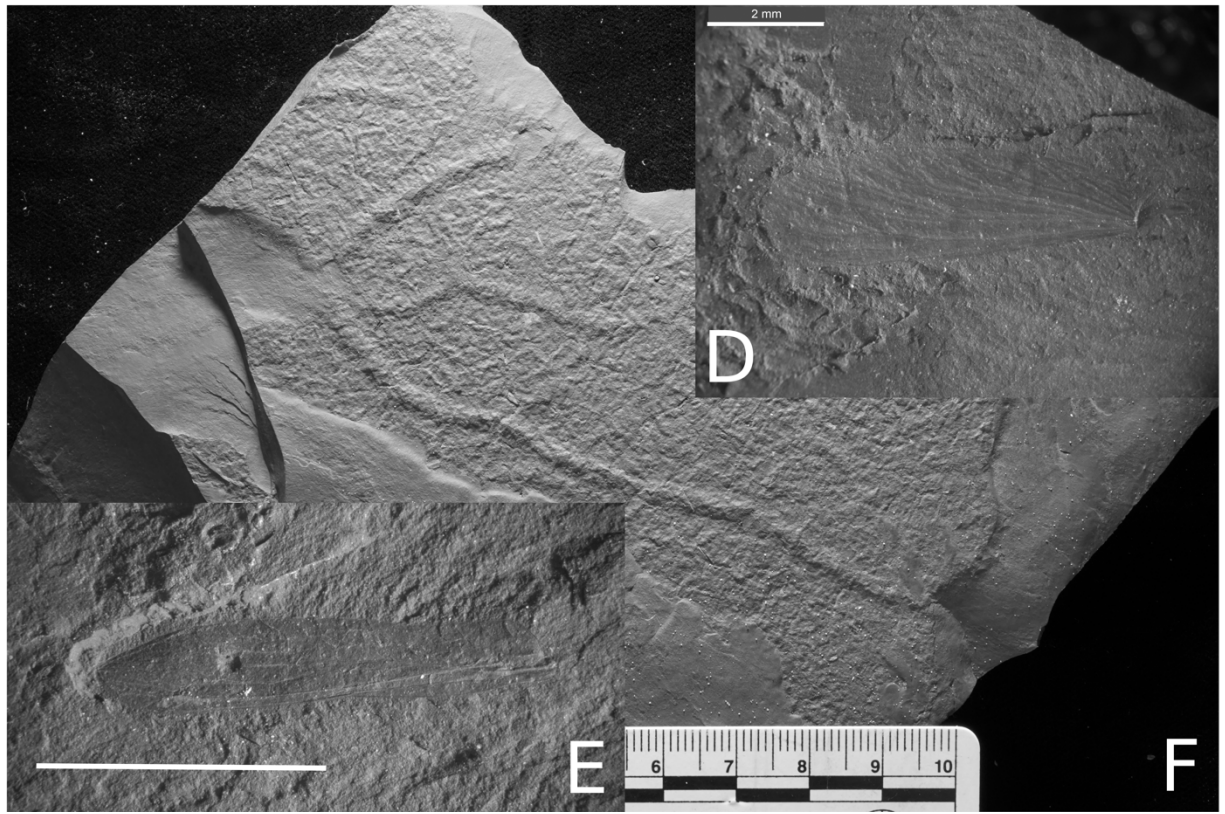
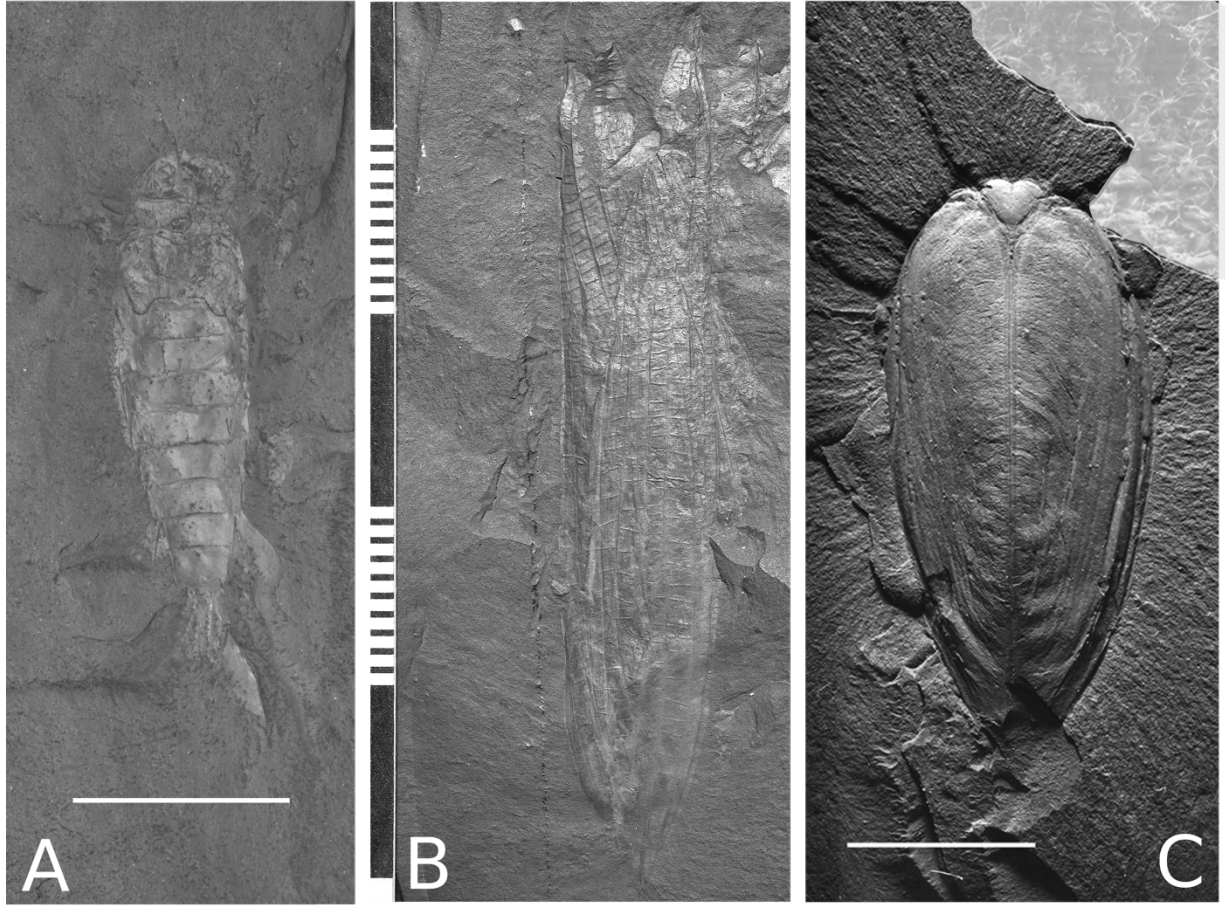


Figure 4. Representative specimens of the angiosperm morphotypes from the Redmond Formation. Morphotype 1 (*‘Andromeda’ novaecaesarae* Hollick): (A) YPM 47190. Morphotype 2 (*‘Andromeda’ parlatorii* Heer): (B) YPM 30413. Morphotype 3 (*‘Aralia’ groenlandica* Heer): (C) YPM 30445, (D) YPM 30384. Morphotype 4 (*Araliopsoides cretacea* (Newberry) Berry): (E) YPM 47191. Morphotype 5 (*Celastrophyllum albaedomus* Ward): (F) YPM 47192. Morphotype 7 (*Cissites formosus* Heer): (H) YPM 47247. Morphotype 8 (*Cissites platanoidea* Hollick): (G) MPEP 702.53, (I) YPM 30423, (J) YPM 30428, (K) YPM 47248. Morphotype 6 (*Celastrophyllum brittonianum* Hollick): (L) YPM 47246. Morphotype 10 (*Daphnophyllum dakotense* Lesquereux): (M) YPM 30471. Morphotype 9 (*Crassidenticulum*): (N) YPM 30492. Scale bars 1 cm or marked in mm. Images adjusted for brightness and contrast. For more information on each morphotype, see Demers-Potvin & Larsson (2019).

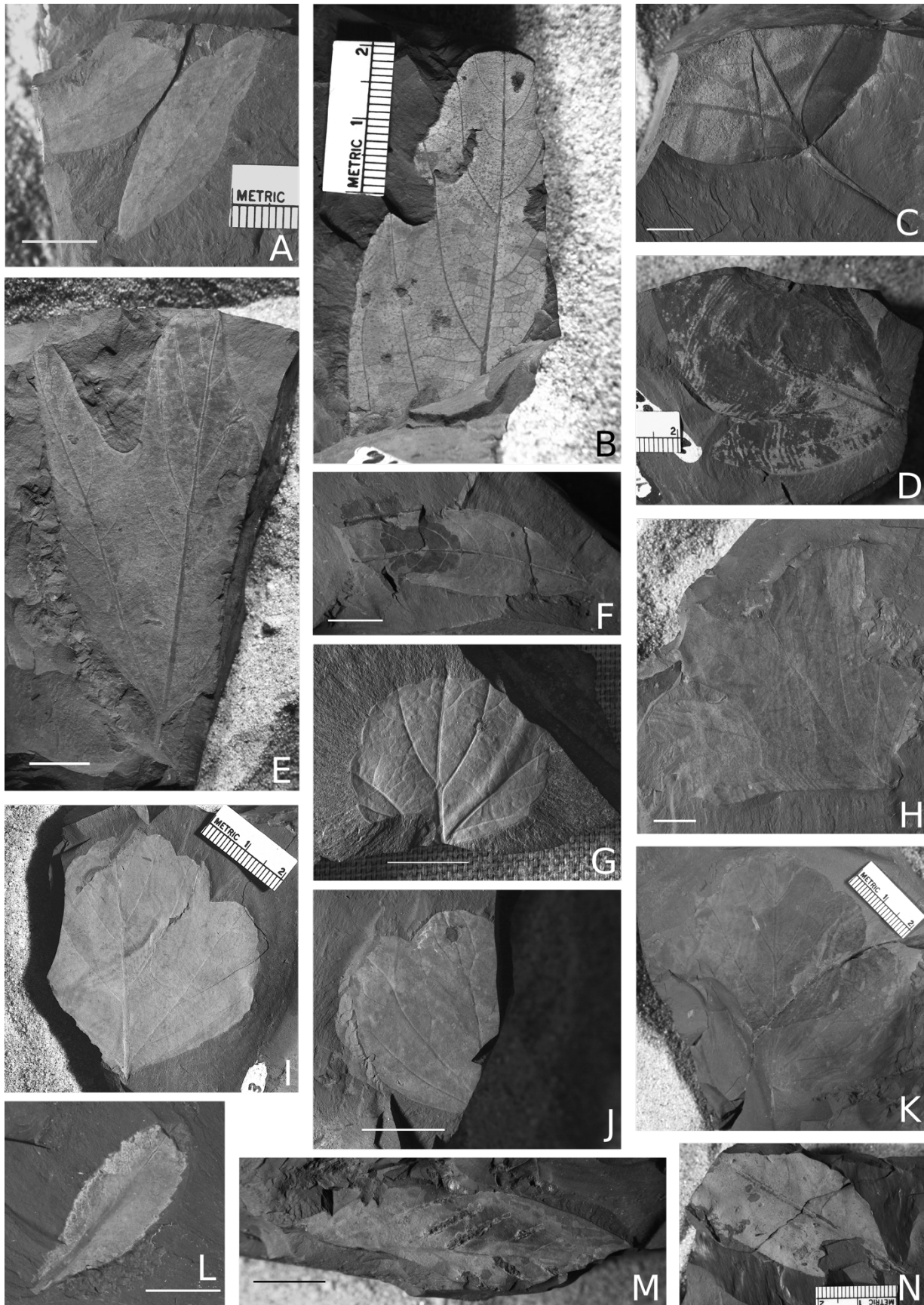


Figure 5. Representative specimens of the angiosperm morphotypes from the Redmond Formation. Morphotype 11 (*Densinervum* *kaulii* Upchurch & Dilcher): **(A)** YPM 30448. Morphotype 12 (*Dicotylophyllum* sp. Indet): **(B)** YPM 30465. Morphotype 13 (*Diospyros* *primaeva* Heer): **(C)** YPM 47249. Morphotype 14 (*Dryandroides lanceolata* Knowlton): **(D)** YPM 47294. Morphotype 15 (*Dryandroides* sp. Indet): **(E)** MPEP 609.6. Morphotype 16 (*Ficus berthoudi* Lesquereux): **(F)** YPM 47296. Morphotype 18 (*Liriodendropsis simplex* (Newberry) Newberry): **(G)** YPM 45137. Morphotype 19 (*Magnolia amplifolia* Heer, *Magnolia speciosa* Heer): **(H)** YPM 30401. Morphotype 17 (*Liriodendron simplex* Newberry): **(I)** YPM 30484. Morphotype 20 (*Magnolia* sp. Indet): **(J)** YPM 30405. Scale bars 1 cm or marked in mm. Images adjusted for brightness and contrast. For more information on each morphotype, see Demers-Potvin & Larsson (2019).

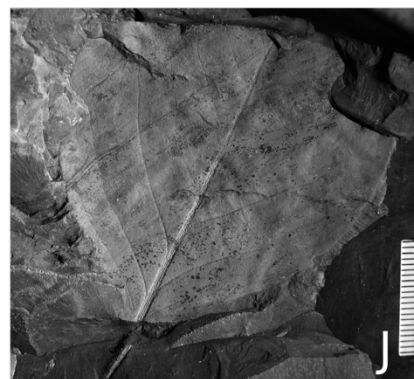
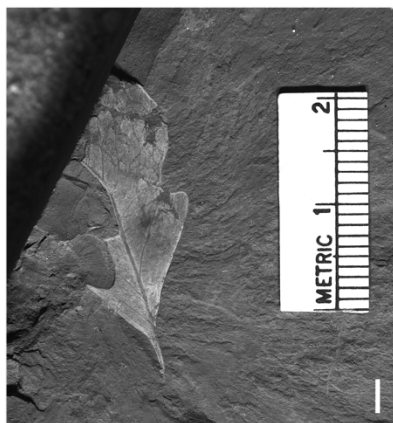
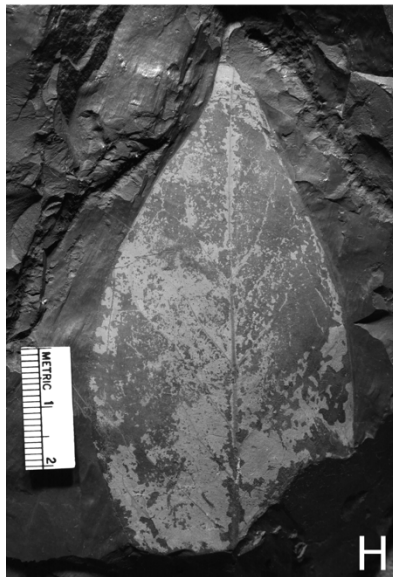
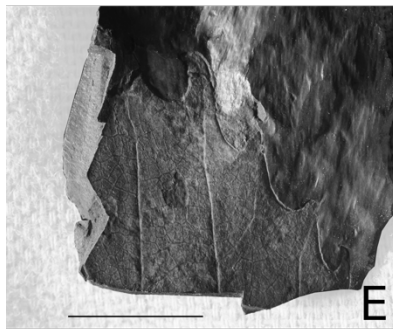
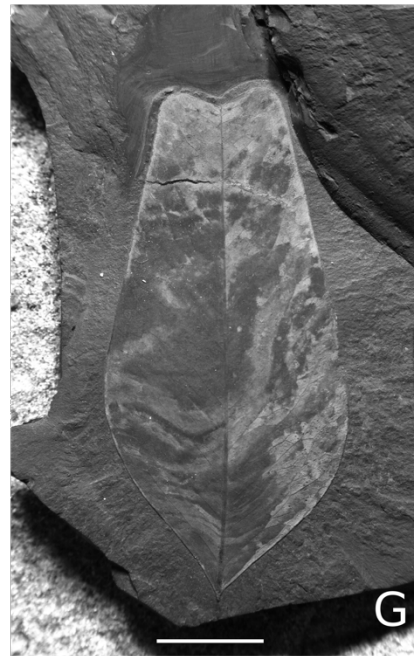
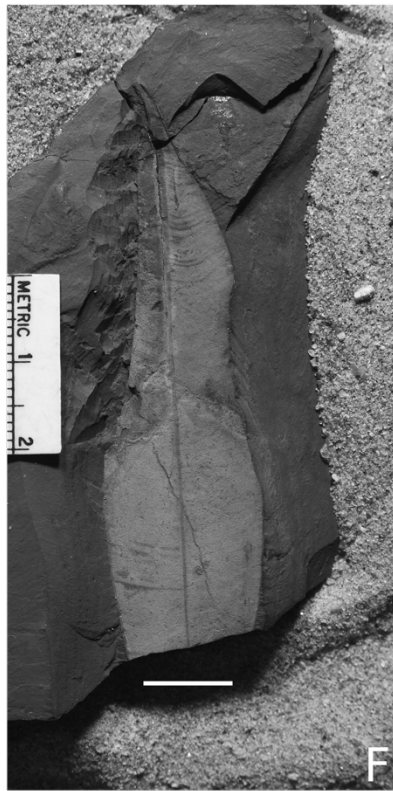
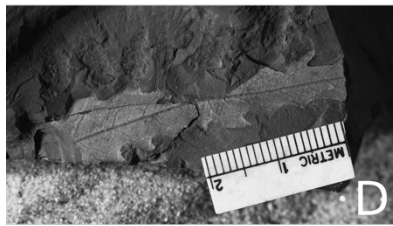
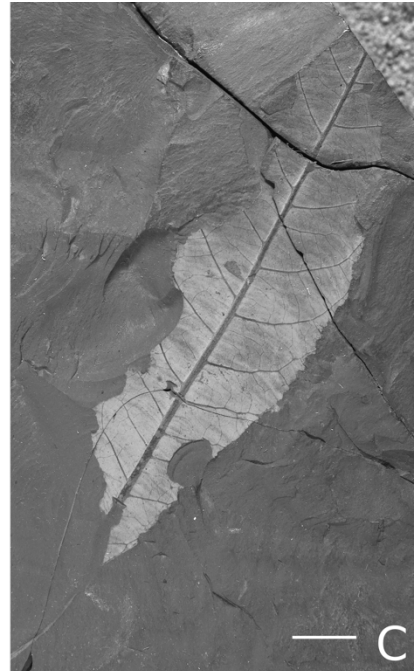
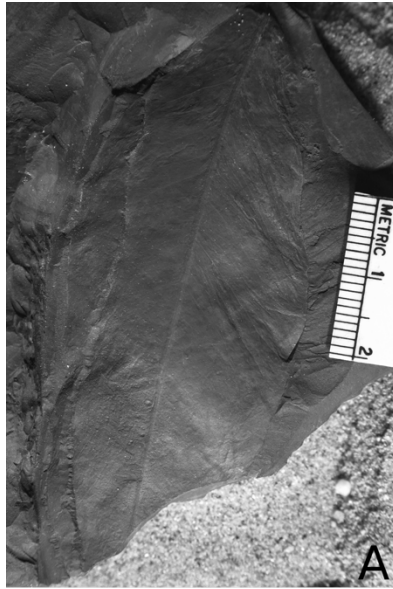


Figure 6. Representative specimens of the angiosperm morphotypes from the Redmond Formation. Morphotype 21 (*Menispermites obtusiloba* Lesquereux): **(A)** YPM 30521. Morphotype 22 (*Menispermites trilobatus* Berry): **(B)** YPM 30516. Morphotype 23 (*‘Platanus’ heerii* Lesquereux): **(C)** YPM 30517. Morphotype 26 (*Sassafras acutilobum* Lesquereux) : **(D)** YPM 30375, **(E)** YPM 30390, **(F)** RMPB 2018.18.27. Morphotype 25 (*Salix newberryana* Hollick): **(G)** YPM 47303. Morphotype 28: **(H)** RMPB 2018.18.9. Morphotype 24 (*‘Platanus’ shirleyensis* Berry): **(I)** YPM 30392. Morphotype 27 (*‘Sterculia’ lugubris* Lesquereux): **(J)** YPM 47299. Morphotype 31: **(K)** RMPB 2018.18.13. Morphotype 29: **(L)** YPM 47300. Morphotype 30: **(M)** YPM 47301. Morphotype 33: **(N)** MPEP 702.59. Morphotype 46: **(O)** MPEP 1177.9. Scale bars 1 cm or marked in mm. Images adjusted for brightness and contrast. For more information on each morphotype, see Demers-Potvin & Larsson (2019).

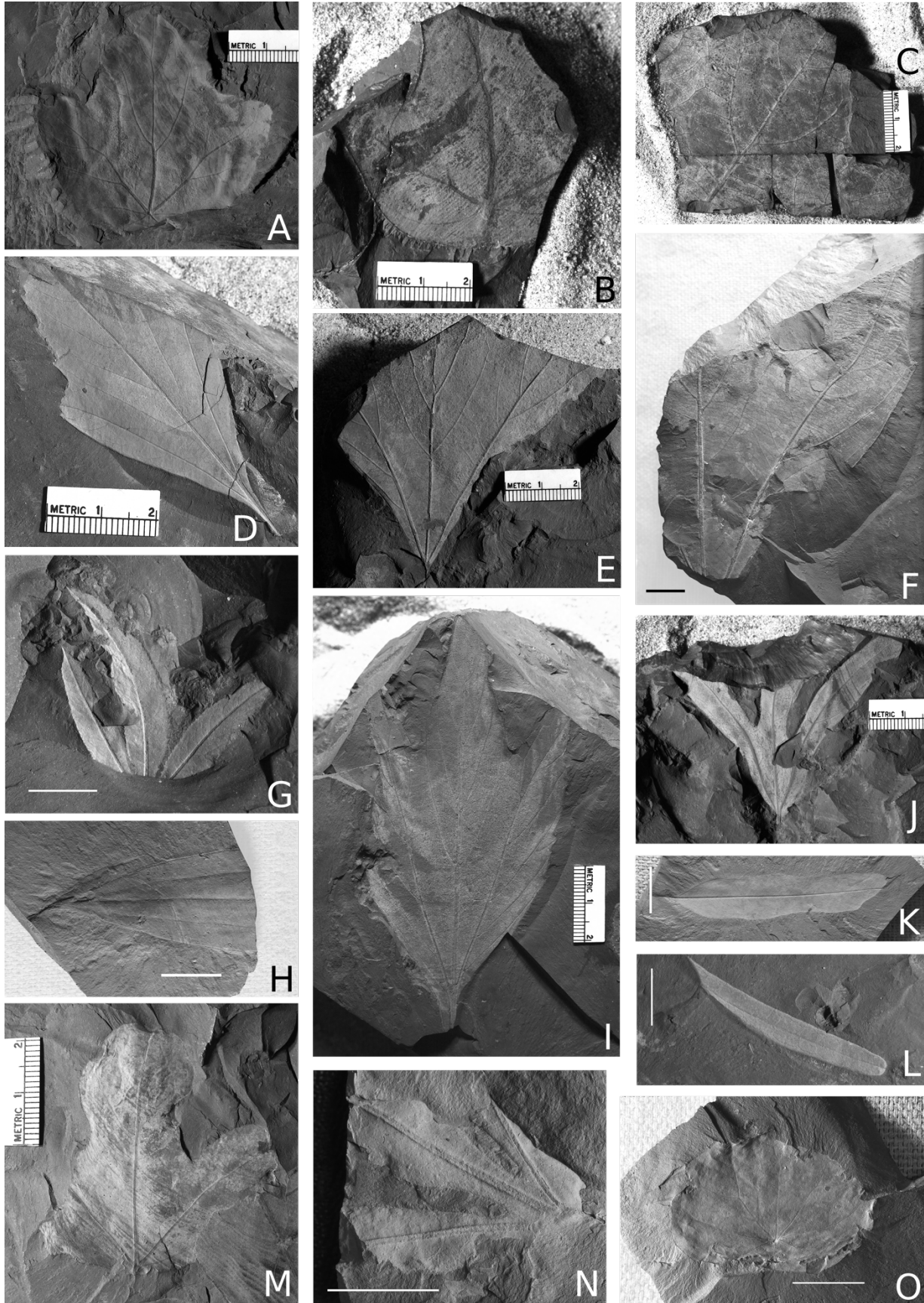


Figure 7. Representative specimens of the angiosperm morphotypes from the Redmond Formation. Morphotype 32: **(A)** YPM 30500. Morphotype 38: **(B)** GSC 104192. Morphotype 35: **(C)** MPEP 702.58. Morphotype 36: **(D)** MPEP 609.1. Morphotype 34: **(E)** MPEP 702.39. Morphotype 37: **(F)** MPEP 702.115. Morphotype 41: **(G)** RMPB 2018.18.2. Morphotype 39: **(H)** RMPB 2018.18.28. Morphotype 45: **(I)** MPEP 1152.27. Morphotype 42: **(J)** RMPB 2018.18.20. Morphotype 40: **(K)** RMPB 2018.18.4. Morphotype 43: **(L)** MPEP 1151.5. Morphotype 44: **(M)** MPEP 1154.5. Scale bars 1 cm or marked in mm. Images adjusted for brightness and contrast. For more information on each morphotype, see Demers-Potvin & Larsson (2019).

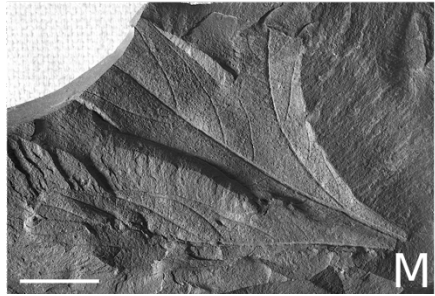
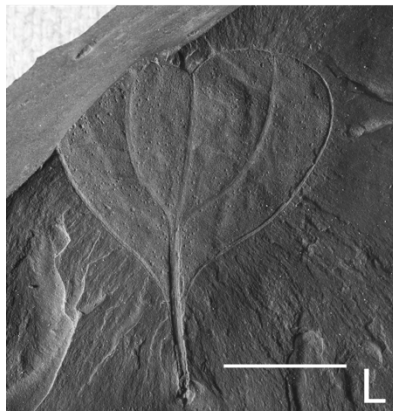
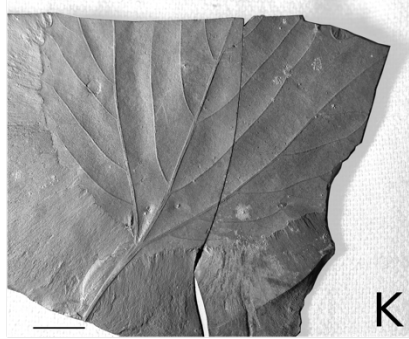
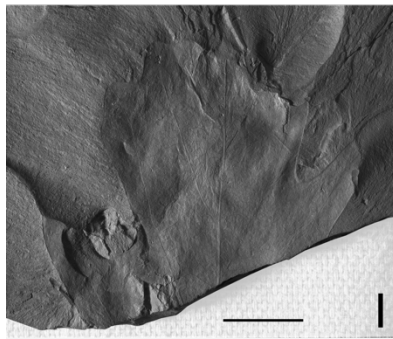
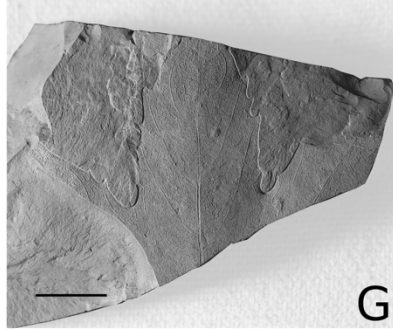
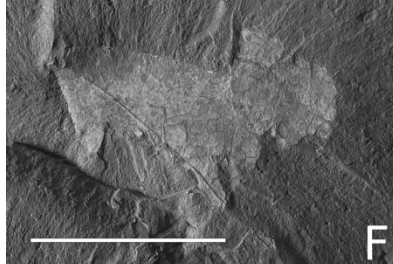
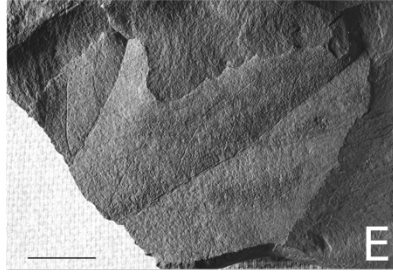
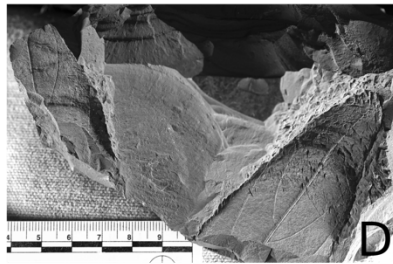
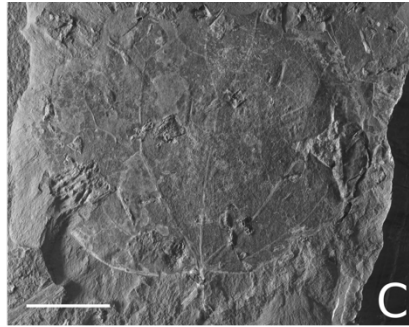
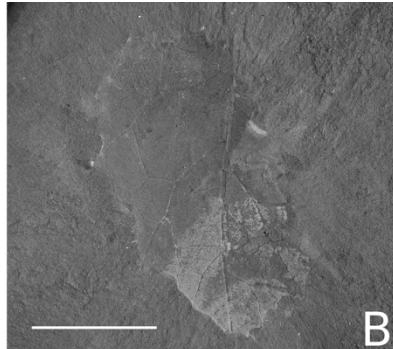
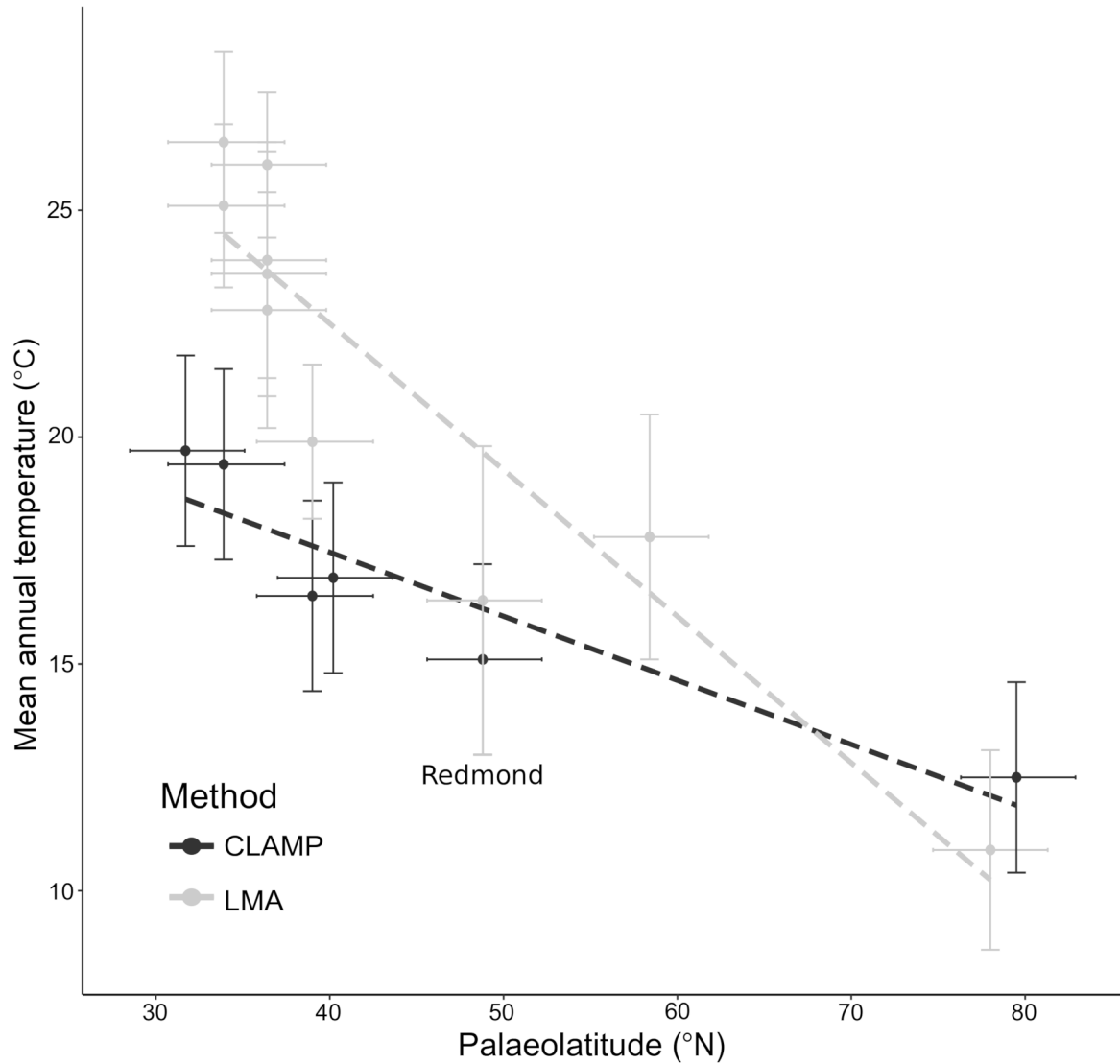


Figure 8. Implied palaeolatitudinal gradients of mean annual temperature for a Cenomanian age bin (93.9 - 100.5 MA) based on two palaeoclimate estimate methods: CLAMP (this study) and LMA (reproduced from Miller *et al.* (2006)). Palaeolatitudes calculated from Van Hinsbergen *et al.* (2015a). In the following list, each flora is succeeded by its estimated palaeolatitude and the source of its palaeoclimate estimate. Raritan (36.4°N) (Wolfe and Upchurch 1987); Patapsco (36.4°N) (Wolfe and Upchurch 1987); Tuscaloosa (31.7°N) (Spicer and Herman 2010); Woodbine (37.4°N) (Wolfe and Upchurch 1987 (LMA); Spicer and Herman 2010 (CLAMP)); Rose Creek (40.2°N) (this study); Fort Harker (Dakota) (39.0°N) (Wolfe & Upchurch, 1987 (LMA); this study (CLAMP)); Redmond (Redmond) (48.8°N) (Hickey and Armstrong 1998 (LMA); this study (CLAMP)); Dunvegan (58.4°N) (Wolfe and Upchurch 1987); Chandler (78.0°N) (Parrish and Spicer 1988); Nanushuk (79.5°N) (Herman *et al.* 2016). Minimum and maximum palaeolatitude estimates for each point projected as error bars. Abbreviations for the methods used are as follows: Climate Leaf Analysis Multivariate Program (CLAMP), Leaf Margin Analysis (LMA). Regression equations – LMA $y = -0.3228x + 35.415$, $R^2 = 0.8576$. CLAMP $y = -0.1412x + 23.109$, $R^2 = 0.8515$.



2.9 Tables

Table 1. Summary of woody dicotyledonous morphotypes used for a palaeoclimate estimate of the Labrador's Cenomanian Redmond ecosystem. *Abbreviations:* ML, mean length; MQI, morphotype quality index; MW, mean width; NA, data unavailable for measurement of calculation; SD, standard deviation (see Harris & Arens 2016 for details).

* Estimates from Armstrong (1993). More information on morphotype classification can be found in Demers-Potvin & Larsson (2019).

Morphotype / systematic affinity	No. specimens	ML / SD (mm)	MW / SD (mm)	MQI
1 <i>Andromeda novaecaesarae</i> Hollick	2	33.4	9.9 / 0.7 (n = 2)	4
2 <i>Andromeda parlatorii</i> Heer	2	84.0* (n = 1)	36.0* (n = 1)	4
3 ' <i>Aralia</i> ' <i>groenlandica</i> Heer	9	57.0 / 1.4 (n = 2)	51.3 / 2.5 (n = 2)	5
4 <i>Araliopsoides cretacea</i> (Newberry) Berry	1	67.8	57.9	7
5 <i>Celastrorhynchium albaedomus</i> Ward	6	54.0 (n = 1)	14.8 (n = 1)	4
6 <i>Celastrorhynchium brittonianum</i> Hollick	2	30.6 (n = 1)	10.2 / 0.0 (n = 2)	7
7 <i>Cissites formosus</i> Heer	3	105.0* (n = 1)	95.0* (n = 1)	5
8 <i>Cissites platanoidea</i> Hollick	28	39.4 / 18.5 (n = 9)	41.0 / 19.8 (n = 10)	7
9 <i>Crassidenticulum</i> sp. indet	8	NA	NA	2
10 <i>Daphnophyllum dakotense</i> Lesquereux	1	53.3	17.6	2
11 ' <i>Densinervum</i> ' <i>kaulii</i> Upchurch & Dilcher	3	NA	NA	2
12 <i>Dicotylophyllum</i> sp. indet	2	39.4 / 0.6 (n = 2)	17.8 / 0.4 (n = 2)	5
13 <i>Diospyros primaeva</i> Heer	4	93.0* (n = 1)	29.0* (n = 1)	4
14 <i>Dryandroides lanceolata</i> Knowlton	1	91.0*	10.0*	5
15 <i>Dryandroides</i> sp. indet	2	NA	NA	4
16 <i>Ficus berthoudi</i> Lesquereux	10	89.0* (n = 1)	25.4 / 6.3 (n = 3)	4
17 <i>Liriodendron simplex</i> Newberry	2	23.8 (n = 1)	14.0 (n = 1)	4
18 <i>Liriodendropsis simplex</i> Newberry	9	31.1 / 13.9 (n = 4)	16.0 / 7.6 (n = 5)	6
19 <i>Magnolia amplifolia</i> Heer, <i>Magnolia speciosa</i> Heer	13	96.1 / 17.3 (n = 4)	46.6 / 9.2 (n = 4)	6
20 <i>Magnolia</i> sp. indet	4	NA	46.3 / 12.8 (n = 3)	4
21 <i>Menispermites obtusiloba</i> Lesquereux	1	58.5	61.6	5

22	<i>Menispermites trilobatus</i> Berry	2	71.0* (n = 1)	69.0* (n = 1)	3
23	<i>Platanus heerii</i> Lesquereux	3	NA	NA	5
24	<i>Platanus shirleyensis</i> Berry	3	78.5 / 54.5 (n = 2)	42.9 / 18.1 (n = 3)	7
25	<i>Salix newberryana</i>	2	5.2 / 29.2 (n = 2)	6.0 / 0.6 (n = 2)	3
26	<i>Sassafras acutilobum</i> Lesquereux	23	54.9 / 7.7 (n = 3)	27.9 / 6.0 (n = 3)	6
27	' <i>Sterculia</i> ' <i>lugubris</i> Lesquereux	1	NA	NA	4
28		1	NA	NA	3
29		3	NA	5.8 / 2.0 (n = 5)	4
30		1	47.4	54.7	4
31		5	NA	10.2 / 2.1 (n = 3)	3
32		1	51.0	45.0	5
33		2	NA	NA	2
34		1	NA	NA	4
35		3	33.1	41.3	5
36		2	NA	NA	4
37		1	NA	16.2	5
38		1	NA	22.3	5
39		1	NA	17.1	4
40		1	NA	NA	5
41		2	NA	NA	4
42		1	NA	NA	5
43		1	16.2	18.3	4
44		1	NA	NA	3
45		1	NA	NA	5
46		1	20.2	28.3	7
Total No. specimens		177	45	66	-

Table 2. Summary of palaeoclimate parameter estimates from the Climate Leaf Analysis Multivariate Program (CLAMP) for the Redmond no.1 site. For CLAMP, all errors are 2σ , and are calculated by treating samples from each modern calibration site as passive (retrieved from Spicer, 2006). GRIDMet, estimates obtained from an analysis that uses a temperate North American gridded meteorological calibration dataset; Met, estimates obtained from an analysis that uses an alternative ungridded North American calibration dataset; Global378, estimates obtained from an analysis that uses a more global gridded calibration dataset (see Spicer 2006; Spicer *et al.* 2009 for more details). *Parameter abbreviations:* CMMT, coldest month mean temperature; ENTHAL, enthalpy; GSP, growing season precipitation; LGS, length of the growing season; MAT, mean annual temperature; MMGSP, mean monthly growing season precipitation; RH, relative humidity; SH, specific humidity; Three DRY, precipitation during three driest months; Three WET, precipitation during three wettest months; WMMT, warmest month mean temperature. See Demers-Potvin and Larsson (2019) for CLAMP physiognomic character state frequencies in scoresheet.

Physiognomic Method Used	MAT (°C)	WMMT (°C)	CMMT (°C)	LGS (Months)	GSP (cm)	MMGSP (cm)
CLAMP (GRIDMet)	15.1 ± 2.1	23.1 ± 2.5	7.8 ± 3.4	8.4 ± 1.1	119.6 ± 31.7	13.6 ± 3.8
CLAMP (Met)	15.4 ± 2.0	23.9 ± 2.7	8.0 ± 3.4	10.7 ± 1.1	153.3 ± 48.3	16.1 ± 5.2
CLAMP (Global378)	13.5 ± 4.0	23.7 ± 3.9	3.4 ± 6.7	9.3 ± 1.9	86.7 ± 54.9	6.0 ± 6.0

Physiognomic Method Used	Three WET (cm)	Three DRY (cm)	RH (%)	SH (g/kg)	ENTHAL (kJ/kg)
CLAMP (GRIDMet)	68.1 ± 22.9	16.6 ± 5.9	71.9 ± 8.6	8.5 ± 1.7	32.1 ± 0.8
CLAMP (Met)	70.5 ± 20.6	27.1 ± 13.7	66.0 ± 11.1	7.4 ± 1.7	30.8 ± 0.6
CLAMP (Global378)	59.8 ± 32.2	7.2 ± 13.0	57.0 ± 9.3	7.4 ± 2.0	31.9 ± 1.1

Table 3. Palaeoclimate estimates for late Albian-Cenomanian North American floras using CLAMP and LMA. LMA standard errors (SE) retrieved from Miller *et al.* (2006, eqn 3). CLAMP (G), estimates calibrated with global gridded climate data using the methodology of Spicer *et al.* (2009). All CLAMP errors are 2σ , and are calculated by treating samples from each modern calibration site as passive (retrieved from Spicer, 2006). *Parameter abbreviations:* CMMT, coldest month mean temperature; GSP, growing season precipitation; LGS, length of the growing season; MAT, mean annual temperature; P.Lat, palaeolatitude; WMMT, warmest month mean temperature. Palaeolatitudes calculated on www.paleolatitude.org (v. 2.1) using the reference frame of Torsvik *et al.* (2012); for more details on the calculator, see Van Hinsbergen *et al.* (2015). See Demers-Potvin and Larsson (2019) for CLAMP physiognomic character state frequencies in scoresheets.

Flora (Formation)	P.Lat (°N) (Min; Max)	MAT reference	Method	MAT (°C) (SE)	WMMT (°C) (SE)	CMMT (°C) (SE)	LGS (Months) (SE)	GSP (cm) (SE)
Woodbridge (Raritan)	36.4 (33.2; 39.8)	Wolfe and Upchurch (1987)	LMA	26.0 (2.7)	-	-	-	-
South Amboy (Raritan)	36.4 (33.2; 39.8)	Wolfe and Upchurch (1987)	LMA	22.8 (4.4)	-	-	-	-
Milton (Raritan)	36.4 (33.2; 39.8)	Wolfe and Upchurch (1987)	LMA	23.9 (4.6)	-	-	-	-
Malden Mtn (Patapsco)	36.4 (33.2; 39.8)	Wolfe and Upchurch (1987)	LMA	23.6 (4.8)	-	-	-	-
Arthurs Bluff (Woodbine)	37.4 (30.7; 33.9)	Wolfe and Upchurch (1987)	LMA	26.5 (3.6)	-	-	-	-
Denton Co. (Woodbine)	37.4 (30.7; 33.9)	Wolfe and Upchurch (1987)	LMA	25.1 (3.0)	-	-	-	-
Fort Harker (Dakota)	39.0 (35.8; 42.5)	Wolfe and Upchurch (1987)	LMA	24.5 (3.9)	-	-	-	-
Dunvegan (Dunvegan)	58.4 (55.2; 61.8)	Wolfe and Upchurch (1987)	LMA	17.8 (4.2)	-	-	-	-
Chandler (Chandler)	78.0 (74.7; 81.3)	Parrish and Spicer (1988)	LMA	10.9 (3.3)	-	-	-	-
Redmond (Redmond)	48.8 (45.6; 52.2)	Hickey and Armstrong (1998)	LMA	19.9 (5.2)	-	-	-	-
		This study	CLAMP (G)	15.1 (2.1)	23.1 (2.5)	7.8 (3.4)	8.4 (1.1)	119.6 (31.7)
Rose Creek (Dakota)	40.2 (37.0; 43.6)	This study	CLAMP (G)	16.9 (2.1)	26.5 (2.5)	8.0 (3.4)	9.1 (1.1)	173.1 (3.8)
Fort Harker (Dakota)	39.0 (35.8; 42.5)	This study	CLAMP (G)	16.5 (2.1)	23.2 (2.5)	10.2 (3.4)	9.1 (1.1)	127.1 (3.8)
Tuscaloosa (Tuscaloosa)	31.7 (28.5; 35.1)	Spicer and Herman (2010)	CLAMP (G)	19.7 (2.1)	24.5 (2.5)	15.1 (3.4)	10.5 (1.1)	145.6 (3.8)
Woodbine (Woodbine)	37.4 (30.7; 33.9)	Spicer and Herman (2010)	CLAMP (G)	19.4 (2.1)	23.5 (2.5)	15.4 (3.4)	10.3 (1.1)	130.5 (3.8)
Nanushuk (Corwin)	79.5 (76.3; 82.9)	Herman <i>et al.</i> (2016)	CLAMP (G)	12.5 (2.1)	20.0 (2.5)	5.7 (3.8)	-	-

BRIDGING TEXT

The last chapter described the successful completion of the first specific objective of the palaeoecological description of the Redmond Formation. Now that the palaeoclimatic reconstruction has been completed, the second specific objective of this thesis must be addressed. It consists in increasing the biodiversity known from the Redmond assemblage through the description of new species. Before this project began, only five insect species were previously described from this locality: a phasmatodean, a hodotermitid termite, a new archostematan beetle, a snakefly (Raphidioptera, Alloraphidiidae), and an antlion (Neuroptera, Myrmeleontidae) (Carpenter 1967; Dorf 1967; Emerson 1967; Ponomarenko 1969; Rice 1969). These are joined by undescribed coleopterans and blattodeans that number 18 specimens altogether. Now, the 2013 and 2018 expeditions to the Redmond no.1 mine have led to the recovery of 570 insect impression fossils. Many of these are sufficiently complete and/or articulated to warrant descriptions, so the potential to increase the biodiversity known from this site is very high.

Even an analysis of functional diversity based on the identification of various isolated wings to known taxa would be beyond the scope of this thesis. The one contribution that can be included here is the first description of a hemipteran for this locality. This particular taxon seems appropriate for inclusion alongside a chapter focusing on angiosperms and climate since true bugs have long been associated with dominant land plants through phytophagy, which resulted in a high turnover during the Cretaceous Terrestrial Revolution (Szwedo 2018). This new cicadomorph is classified in Tettigarctidae, one of the many hemipteran families that shifted their host preference from gymnosperms to angiosperms as the latter radiated (Labandeira 2014). It represents the first tettigarctid occurrence in the entire North American fossil record, which adds significant information on the biogeographical history of this family. It also confirms the widespread distribution of tettigarctids throughout the Mesozoic, which contrasts sharply with their current distribution as a relict taxon.

CHAPTER 3. First North American occurrence of hairy cicadas discovered in the Late Cretaceous (Cenomanian) Redmond Formation, Labrador, Canada

Abstract

We report the discovery of *Maculaferrum blaisi* gen. et sp. nov, the first occurrence of the family Tettigarctidae, informally known as hairy cicadas, in North America. *M. blaisi* is part of a new collection assembled during recent fieldwork in the Redmond Formation, Labrador, Canada, near Schefferville. It consists in a single isolated forewing whose venational characters allow a classification to Tettigarctinae at the subfamily level. Classification at a higher level remains uncertain since it displays a combination of characters supposedly unique to tribes Protabanini, Meunierini and Tettigarctini. Thus, this discovery adds credence to suggestions of a revision of the definitions of these tribes since they seem based on many convergent or plesiomorphic characters. Remnants of a spotted pattern on the wing membrane and probable setae along some veins are also preserved. Observations of the holotype's fine anatomical characters have been facilitated by the use of Reflectance Transformation Imaging (RTI), an emerging method for the visualization of compression and impression fossils. Considering that the estimated age of the Redmond Formation is the Late Cretaceous (Cenomanian), the discovery of *M. blaisi* contributes to a very recent expansion of the tettigarctid fossil record that fills a gap between Early Cretaceous and Cenozoic genera. It suggests that hairy cicadas maintained a global distribution and thrived in a variety of climate regimes well into the Late Cretaceous, and that their competitive exclusion by singing cicadas occurred definitely closer to the end of the Cretaceous, or even during the Cenozoic. This discovery is only the start of a thorough description of the recently expanded entomofauna of Cretaceous Labrador.

3.1 Introduction

Tettigarctidae (hairy cicadas) were the dominant family within Cicadoidea for much of the Mesozoic (Shcherbakov 2009; Moulds 2018). They are distinguished from sister family Cicadidae (modern singing cicadas) by a greatly expanded pronotum covering much of the mesonotum, forewings with a conspicuous nodal line, a posterior radial sector (RP) emerging closer to the wing base than to the node, all anal veins running separately, male genitalia with styles, hind coxae

overhanging the abdomen, the presence of tarsal empodia, absence of tympana, and a nervous system with separated thoracic ganglia (Evans 1941; Moulds 2005, 2012). Another distinctive tettigarctid character is the presence of rudimentary tymbals that produce low-intensity, substrate-transmitted acoustic signals, instead of well-developed tympanal auditory organs that lead to loud airborne calls characteristic of singing cicadas (Claridge et al. 1999).

Today, Cicadidae number nearly 2900 species worldwide (Bartlett et al. 2018) as a result of a radiation that probably occurred in the Palaeogene (Kaulfuss and Moulds 2015), while Tettigarctidae are represented by only two species of *Tettigarcta* White, 1845: *T. crinita* Distant, 1883 in Southeastern Australia, and *T. tomentosa* White, 1845 in Tasmania. Both species are restricted to cool subalpine forests to which they are adapted with dense insulating hairs, and have a nocturnal habit unique among extant cicadoids (Claridge et al. 1999; Shcherbakov 2009). This is a very specialized lifestyle in a far more restricted range than that occupied by this once diverse family in the Mesozoic (Boulard and Nel 1990; Zeuner 1944). While the diet of tettigarctids shifted from gymnosperm to angiosperm herbivory, likely in response to the floral turnover that occurred in the middle of the Cretaceous, cicadids seem to have appeared at the peak of this angiosperm radiation and retained them as hosts throughout their history (Labandeira 2014). This may have conferred cicadids a competitive advantage resulting in the displacement of tettigarctids from most of their original range until a single lineage remained in biogeographical isolation in Southern Australia (Zeuner 1944; Wang & Zhang 2009).

Until recently, the tettigarctid fossil record contained 29 genera and 46 species spread into subfamilies Cicadoprobolinae and Tettigarctinae (Moulds 2018; Fu *et al.* 2019; Jiang *et al.* 2019; Lambkin 2019). The oldest members of the family are *Mesodiphthera grandis* Tillyard, 1919, *Tardilly prosboloides* (Tillyard, 1922) and *Tardilly dunstani* (Tillyard, 1922) from the Late Triassic (Norian) of Dinmore, Queensland, Australia. The youngest is *Paratettigarcta zealandica* Kaulfuss and Moulds, 2015 from the early Miocene of Hindon Maar, New Zealand. The Jurassic has the highest tettigarctid diversity of any period, although it is restricted to Laurasia and represented largely by species from the Yanliao (Daohugou) Biota (Moulds 2018). Some of these reached far larger body sizes than modern species (Chen and Wang 2016), while others had already evolved patterns of disruptive colouration (Chen et al. 2016; Zheng et al. 2016) and dense body hairs that were initially thought to be unique to modern *Tettigarcta* (Liu et al. 2016). The known family diversity decreases in the Early Cretaceous, but has a more global distribution, with the first

occurrences in former Gondwanan landmasses: *Architettix compacta* Hamilton, 1990 and *Tettagalma striata* Menon, 2005 from the Crato Formation of Brazil, and *Magrebarcta africana* Nel, Zarbout, Barale and Philippe, 1998 from the Duriet Formation of Tunisia. Not a single hairy cicada was known from the Late Cretaceous until the discovery of three new species in the earliest Cenomanian amber deposits of Kachin, Myanmar: *Cretotettigarcta burmensis* Fu, Cai and Huang, 2019, *Vetuprobole parallelica* Fu, Cai and Huang, 2019, and *Hpanraais problematicus* Jiang, Chen, Jarzembowski and Wang, 2019. Their unique location and relatively ancestral character states supported the hypothesis of Southeast Asia as a Late Cretaceous tropical refuge based on the occurrence of other rare insect taxa.

In this paper, we report the discovery of *Maculaferrum blaisi* gen. et sp. nov., the first tettigarctid known from North America. It was found during a recent expedition to the Redmond no.1 mine, located in Labrador, Canada, near Schefferville. This abandoned iron ore mine contains lacustrine deposits that represent the only known exposures of Cretaceous rocks in the entire Quebec-Labrador Peninsula (Blais 1959; Dorf 1967). The expedition led to the discovery of more fossil leaf morphotypes and potentially new insect species. *Maculaferrum* is the first of these newly discovered insects to be formally described.

Institutional abbreviations. – MNHN, Muséum national d’histoire naturelle, Paris, France; MPE, Musée de paléontologie et de l’évolution, Montreal, Canada; NMV, National Museums Victoria, Melbourne, Australia; RM, Redpath Museum, Montreal, Canada.

Other abbreviations. – A, anal vein; a, apical cell; av, ambient vein; bc, basal cell; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M₁₊₂, two anterior branches of M; M₃₊₄, two posterior branches of M; m, medial cross vein; mc, medial cell; m-cu, mediocubital cross vein; RA, radius anterior; RP, radius posterior; r, radial cross vein; r-m, radio-medial cross vein; Sc, subcosta; u, ulnar cell.

Nomenclatural acts. – This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:act:3A344D5D-9F06-419F-B78D-2170A5947333

3.2 Material and method

The Redmond no.1 mine is located at coordinates of 54°41'N and 66°45'W, Labrador, Canada, 16 km south southeast of Schefferville (Fig. 1). This site remains the only known exposure of the Redmond Formation, a basin surrounded by Palaeoproterozoic rocks that was 1524 m long, 508 m wide, and up to 183 m deep when first surveyed in 1957 before becoming out of geological context due to mining activities (Blais 1959). Apart from carbonized wood fragments of cupressacean affinity, the fossils found in this basin were restricted to impressions in a 1.5 m thick bed composed of a hard, very fine-grained, evenly laminated ferruginous argillite of umber colour (Blais 1959; Dorf 1967). The uncovered palaeoflora comprised a few fern, conifer and lycopod specimens, dominated by angiosperm tree leaves that enabled palaeobotanist Erling Dorf to produce a Cenomanian age estimate based on biostratigraphic correlation and to suggest a warm temperate and fully humid climate for the region (Dorf 1959). The insect discoveries were scarce, but still led to the description of five unique and well-preserved specimens: the raphidiopteran *Alloraphidia dorfi* Carpenter, 1967, the hodotermitid *Cretatermes carpenteri* Emerson, 1967, the archostematan beetle *Labradorocoleus carpenteri* Ponomarenko, 1969, the (possibly) myrmeleontid *Palaeoleon ferrogeneticus* Rice, 1969, and the phasmatodean *Palaeopteron complexum* Rice, 1969. In addition, a few blattodean isolated wings (Dorf 1967), some elytra assigned to water beetles (Schizophoridae), and two elytra assigned respectively to Cupedidae and to the haliplid *Peltodytes* sp. (Ponomarenko 1969) have also been mentioned. Despite this meagre collection, the occurrence of taxa rarely preserved in the insect fossil record suggested that many more awaited discovery in the Redmond Formation.

The site was not explored until an expedition by the Musée de paléontologie et de l'évolution (MPE) in summer 2013, by which time mining activities had fragmented the Redmond Formation into small flat claystones scattered among rubble piles (Fig. 1). In August 2018, the first author set out on a longer expedition organized jointly by the Redpath Museum (RM) and the MPE. The discovery of yet more fossil leaves in these two expeditions led to an absolute palaeoclimate estimate that encompassed the entire known angiosperm flora, and that confirmed Dorf's initial relative palaeoclimate and dating hypotheses (Demers-Potvin & Larsson 2019). This fieldwork also led to a significant expansion of the known entomofauna from the site, including the discovery of near-complete nymphs and aquatic coleopterans that strengthened the initial

hypothesis of a lacustrine depositional setting (Blais 1959; Dorf 1959; Demers-Potvin & Larsson 2019).

Among the diverse terrestrial entomofauna preserved in the Redmond Formation was a rare representative of Tettigarctidae. The sole specimen was found on a small thin slab (~6 cm wide × 10 cm long × 0.7 cm deep) of argillite of burgundy colour enriched in iron oxide, among similar pieces of float. Amid this recently assembled entomofauna, we have looked for hind wings that could potentially belong to this genus or a relative within the family, but the most similar ones clearly belonged to leafhoppers (Cicadomorpha: Cicadellidae).

The slice of argillite in which the specimen was found was cut to a 3 cm × 3 cm square using a Lortone lapidary trim saw, Model FS8. The specimen was drawn and photographed at the Centre de recherche sur la Paléobiodiversité et les Paléoenvironnements (MNHN, Paris). A draft drawing was done with a microscope equipped with a camera lucida (Zeiss SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10 × / 23 eye pieces, a Plan Apo S 1.0 × FWD objective; all from Zeiss). The drawing was finalized using Adobe Illustrator CC 2019 using the draft drawing and photographs.

A Reflectance Transformation Imaging (RTI) file was built out of a set of photographs to enhance the 3D contrasts in the impression fossil that facilitate its observation, and to produce composite photographs of superior quality. Photographs were taken using a Canon EOS 5D Mark III digital camera with a Canon MPE-65 macro lens (without polarizing filters). The photographs were taken under a Portable Light Dome, optimized and processed using Adobe Camera Raw and Adobe Photoshop CC 2019, and compiled into an RTI file using the RTI Builder software v. 2.0.2 (freely available under GNU license, using the HSH fitter; see Béthoux et al. 2016; RTI 2019 for more details). We provide the RTI file along with viewer software and instructions (See Supplementary Material). The photographs of RMIP 2018.18.24 included in this paper have all been extracted from the RTI files.

The forewing representing *Maculaferrum blaisi* gen. et sp. nov was also compared with those of the only two extant ‘hairy cicada’ species, *Tettigarcta crinita* and *T. tomentosa*. Habitus and individual forewing photographs were taken for specimens of each species (*T. crinita*: one male (NMV HEM5660); *T. tomentosa*: one male (NMV HEM472) and one female (NMV HEM476)) with a Nikon D5300 enhanced with an AF-S Micro Nikkor 105 mm macro lens in the Entomology collections of NMV. ~20 images per view were taken and subsequently stacked and

optimized using Adobe Photoshop CC 2018. The wing venation terminology follows that of Moulds (2005). Vein M in this terminology is equivalent to vein MP, as MA is always totally fused with RP, which is a synapomorphy of Hemiptera (Bourgoin et al., 2015; Kukulová-Peck, 1991; Nel et al., 2012, 2013).

3.3 Results

3.3.1 Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Cicadomorpha Evans, 1946

Superfamily Cicadoidea Latreille, 1802

Family Tettigarctidae Distant, 1905

Subfamily Tettigarctinae Distant, 1905

Tribe Protabanini Hong, 1982 (?)

Genus *Maculaferrum* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:3A344D5D-9F06-419F-B78D-2170A5947333

Etymology: Generic name derived from Latin *macula*, ‘spot’, referring to the apparent spotted pattern observed on parts of the wing membrane, and Latin *ferrum*, ‘iron’ referring to the high iron content that confers the matrix a distinctive reddish colour.

Type and only species: *Maculaferrum blaisi* sp. nov.; by monotypy, see below. LSID:

urn:lsid:zoobank.org:act:3A344D5D-9F06-419F-B78D-2170A5947333

Diagnosis. – As for the type species by monotypy.

Maculaferrum blaisi sp. nov.

Figs. 2, 3, 4A

Zoobank LSID: urn:lsid:zoobank.org:act:

Etymology: Specific epithet is given in reference to Roger A. Blais, who undertook the initial survey of the Redmond Formation in 1957.

Type material: Holotype, RMIP 2018.18.24 (part), impression of a single isolated forewing either ripped in half or folded onto itself so that the middle area is hidden from view. The basal part

consists in the majority of the pre-nodal area, and the apical part consists in the vast majority of the post-nodal area.

Type locality: Redmond no.1 mine, near Schefferville, Labrador, Canada.

Type horizon: Redmond Formation, Cenomanian, Late Cretaceous.

Diagnosis: In general view, forewing similar to forewing of Protabanini fossils – *Tettagalma striata* Menon, 2005 from the Aptian Crato Formation of Brazil and *Protabanus chaoyangensis* Hong, 1982 from the Jiulongshan Formation, Liaoning, China. Costal cell narrower basally than basal cell (as in *Tettagalma*; in *Protabanus* costal cell about as wide as basal cell); single terminal RP longer than cell a6 (as in *Protabanus*; in *Tettagalma* cell u3 distinctly shorter than cell a6); apical portion of stem CuA basad of nodal line minimally curving mediad (as in *Protabanus*; in *Tettagalma* this section of stem CuA is distinctly curved mediad); CuA₂ with a sharp uniform curve apically (contrary to at most faint apical curves in *Protabanus* and *Tettagalma*). Specimen also resembling some Meunierini, viz. *Meuniera haupti* Piton, 1936 from the Palaeocene quarry of Menat, France, and members of Tettigarctini such as extant *Tettigarcta* spp. from Southern Australia, due to M and CuA joined by a m-cua cross vein at the apical extremity of the basal cell and CuA₂ running along nodal line up to clavus apex. However, it differs from Meunierini due to stem M forking closer to nodal line than to wing base; it also differs from Tettigarctini due to forking of RA not level with cross vein r and CuA₂ curving towards apex instead of base. Uniform curvature of CuA₂ seems apomorphic for *Maculaferrum* gen. nov. Round darker markings in apical cells, less distinct rounded spots in ulnar cells; appendix with minuscule striae (corrugations) exceeding ambient vein; punctate pattern on basal portion of forewing.

3.3.2 Description

Total forewing length estimated at 20-23 mm; maximal forewing width 7.5 mm. Marginal membrane (appendix) present along entire margin apical of RA₁ to 1A terminal apex; ambient vein perfectly visible, criss-crossed by minuscule striae, from RA₂ to CuA₂ (Figs. 2, 3A-B); postclaval membrane present, narrow. Rows of tubercles present along segments of longitudinal veins, each projecting perpendicular to vein (Fig. 3C). Only short segment of the nodal line appears visible, parallel to CuA₂ (Fig. 3D-E). Round to oblong patches present in apical cells a1 to a8 and postnodal

portion of ulnar cells u1 to u3 and medial cell, closer to cross veins (Figs. 2, 3F). Punctate pattern observed on much of pre-nodal area but absent from post-nodal area (Figs. 2, 3G).

Costal area of forewing straight at base, increasingly curved apically, apex relatively sharply curved, claval margin straight, apex of clavus slightly exceeding half of forewing length. Costal margin thick, veins of costal complex flattened to level of nodus. Stem vein Sc tightly adjoined and subparallel to stem R+M, fused with R+M merely apicad of apex of basal cell. Stem Sc+R short, about $\frac{1}{4}$ of length of basal cell, forked distinctly basad of nodal line and M forking; branch of Sc+R subparallel to costal margin, its prenodal section about 3 times as long as stem Sc+R; terminal Sc short, oblique, diverged slightly apically of nodal line. Branch RA forked at basal half of membrane, with three terminals: branch RA₁₊₂ slightly sinuous, RA₁ short, oblique, RA₂ subparallel to forewing anterior margin, RA₁ and RA₂ terminal apices distinctly basad of forewing apex; RA₃ reaching ambient vein slightly basad of forewing apex; RP forked from Sc+R basad of 0.3 of forewing length, reaching ambient vein with single terminal slightly basad of forewing apex. Stem M forked close to nodal line level (Fig. 3H, not clearly preserved), branch M₁₊₂ forked apicad of branch M₃₊₄ forking and apicad of RA forking; M₃₊₄ forked basad of RA forking. Stem CuA leaving basal cell distinctly curved at base, then arcuate, geniculately bent posteriad at nodal line, forked at level of nodal line; branch CuA₁ much longer than branch CuA₂, subparallel to branch M₃₊₄, then bent to ambient vein, to reach it at level of RA forking. CuP and claval fold straight, reaching margin merely basad of nodal line; 1A slightly sinuate, subparallel to CuP; 2A arcuate, relatively short; 3A fused to basal margin of forewing. Cross vein r slightly apicad of terminal RA₁; cross vein r-m oblique, at level of terminal RA₁; cross vein m oblique, connecting M₁₊₂ with terminal M₃, slightly basad of terminal RA₁; basal cross vein m-cua very short, connecting stem M with stem CuA at posterior apical corner of basal cell; apical cross vein m-cua oblique, connecting terminal M₄ with CuA₁ distinctly basad of terminal RA₁, basad of half of M₄ length, apicad of half of CuA₁ length. Basal cell about 4 times as long as wide, subrectangular. Costal cell about as wide as basal cell. Prenodal portion of cell u1 shorter than postnodal portion. Prenodal portion of cell u3 short (not clearly preserved). Cell a7 significantly shorter than other apical cells. Cell a8 slightly shorter than adjoining postnodal portion of cell mc.

Remarks: During fossilization, the forewing was broken along the nodal line, and portions partly overlap. It means that much of the area surrounding the nodal line is not clearly preserved. It is very difficult to see the position of the branching of M into M₁₊₂ and M₃₊₄, but it seems to be very

close to the margin of the preserved basal portion of the forewing. Considering the incomplete state of the specimen, a reconstruction of the entire forewing is presented alongside wings of living relatives *Tettigarcta crinita* and *T. tomentosa* (Fig. 4).

Stratigraphic and geographical range. – Type locality and horizon only.

3.4 Discussion

Maculaferrum blaisi gen. et sp. nov. belongs to family Tettigarctidae based on the following characters: costal cell present, about as wide as basal cell; branch RP arising basally, closer to base than to node; 1A separated from CuP, veins 2A and 3A separated at least at base; nodal line distinct; clavus exceeding half of forewing length; basal portion of forewing punctate. It can be placed further in subfamily Tettigarctinae based on the following characters (Shcherbakov 2009): basal cell wide, not narrowed to apex; costal cell relatively narrow (only slightly narrower than intercubital area); forewing apex sharply curved; very short basal m-cua closing basal cell; apical cell basad of CuA₂ either very narrow or absent (in the case of this new genus); apex of clavus slightly exceeding half of forewing length. The latter character is also found in some taxa placed in Cicadoprosobolinae and could not be diagnostic; further analyses are necessary to assess the importance of this feature. In addition, *M. blaisi* seems to share with other members of Tettigarctinae a cross vein r closer to the wing apex than to the nodal line. This character cannot be observed directly in the specimen since the nodal line is not preserved for most of the wing's width, so it is only implied here (see Remarks; Figs. 2 and 4). *M. blaisi* can be assigned to tribe Protabanini based on the following characters (Shcherbakov 2009): presence of very short basal m-cua closing basal cell; cross vein r reclined; anteriormost apical cell (a₀, between RA₁ and RA₂) narrow triangular; distal section of CuA geniculately bent at nodal line, prolonged by CuA₂; nodal line at or beyond mid-wing; forking of stem M far closer to nodal line than to wing base, implied due to lack of preservation of nodal line (see Fig. 4). Only the a₀ cell character seems truly unique to Protabanini, while the other characters can also be observed on numerous members of Cicadoprosobolinae, such as *Architettix compacta* Hamilton, 1990 (Architettigini; Aptian, Crato Formation, Brazil), Turutanoviini – species of the genus *Sanmai* Chen, Zhang, H., Wang B., Zheng, Wang, X. and Zheng, X., 2016, *Hirtaprosbole erromera* Liu, Li, Yao and Ren, 2016, *Shuraboprosbole daohugouensis* Wang and Zhang, 2009, *Tianyuprosbole*

zhengi Chen, Wang, B., Zhang and Wang, X. 2014 (all from the Callovian/Oxfordian Middle/Late Jurassic Daohugou Formation of North-eastern China); and Cicadoprosobolinae genera unassigned to tribes – *Vetuprosbole* and *Hpanraais* (both from earliest Cenomanian, Late Cretaceous Kachin amber of Myanmar). *Maculaferrum blaisi* gen. et sp. nov. also shares with the aforementioned Jurassic taxa Sc + R significantly shorter than Sc + RA, and m-cu connecting CuA₁ to M₄. It seems to share with members of Protabanini a stem M curving mediad just before bending geniculately along the nodal line. In this respect, M curves relatively minimally in this new genus (as in *Protabanus chaoyangensis* Hong, 1982 or *Sunotettigarcta kudryashevae* Shcherbakov, 2009) instead of curving sharply (as in *Tettagalma*). However, even this character is present in some Cicadoprosobolinae, most notably *Hpanraais*.

Several features observed on the specimen seem to exclude it from Protabanini, as originally defined (Shcherbakov 2009). These are M and CuA joined by a m-cua cross vein in the apical extremity of the basal cell (instead of cross-joining at that extremity) and CuA₂ running along nodal line up to clavus apex (instead of a divergence of the distal section of CuA₂ from the nodal line). These traits are more characteristic of taxa classified in Meunierini (such as *Meuniera haupti* Piton, 1936) and Tettigarctini (such as *Tettigarcta*). The new genus and species shares with Meunierini a forking of RA level with a forking of M₁₊₂ (Shcherbakov 2009). However, it differs from Meunierini due to the forking of stem M at unequal distances from the wing base and nodal line, and it differs from Tettigarctini due to the forking of RA not level with cross vein r (Shcherbakov 2009) and CuA₂ curving towards the apex instead of the base (Fig. 4). Consequently, *Maculaferrum blaisi* gen. et sp. nov. presents a combination of characters supposedly diagnostic of Protabanini, Meunierini and Tettigarctini. Thus, its affinities to a particular tribe within Tettigarctinae remain obscure, and a similar condition has been noted in its contemporary *Cretotettigarcta burmensis* (Fu *et al.* 2019). Together, these recently described genera could contribute to a revision of the definitions of tribes within Tettigarctinae (such as Protabanini), since they seem based on many convergent or plesiomorphic characters.

3.4.1 Interpretation of spotted and filamentous patterns on the wing membrane

The presence of minuscule tubercles along the veins suggests that setae or bristles were present on the forewing of *Maculaferrum blaisi* gen. et sp. nov. (Fig. 3C). Such setae are preserved in extant relative *Tettigarcta*. They have also been observed in extinct relatives (not ascribed to

tribes) preserved in Cenomanian, Late Cretaceous Kachin amber of Myanmar, e.g. *Hpanraais*, *Cretotettigarcta* and *Vetuprosbole*. It must also be noted that the clear delineation between a punctate pattern on the pre-nodal area and a smoother pattern on the post-nodal area is very similar to that observed in *Tianyuprosbole* (Chen *et al.* 2014).

The presence of patches on the apical portion of the forewing of *Maculaferrum* probably does not result from taphonomical bias. Instead, they may indicate a spotted pattern that was actually present on the wing. However, since *Maculaferrum* is represented by an impression fossil, the origin of this pattern is far more nebulous than in a compression fossil, and the lack of distinct pigmentation means that the wing's original colouration pattern may not be fully preserved. This means that any interpretation of this observation must be treated with extreme caution. Spotted patterns are occasionally observed in some *Tettigarcta* individuals, although they are found along the veins and seem less extensive than in *Maculaferrum* (Fig. 4). Of the limited sample of *Tettigarcta* individuals available for this study, such a pattern was only found on the female *T. tomentosa* (Fig. 4C). A future study could aim to compare wing colouration patterns more systematically between sexes among both extant species. Similar patterns are also infrequently present among extant singing cicadas Cicadidae (Distant 1889, 1914; Emery *et al.* 2017). Lighter spots in cells on a dark background are present in species of the genus *Ambragaeania* (Gaeanini) Chou and Yao, 1985. Darker spots on a transparent background, but distributed on veins and adjoining cells, are present in *Kamalata pantherina* Distant, 1889 (Cicadini); more irregular patches on veins and adjoining portions of cells are also present in other Cicadini (Distant 1889, 1912). In contrast, cryptic colouration or patterns of disruptive colouration (speckles and longitudinal stripes) are frequently observed in extinct Tettigarctidae, such as in *Liassocicada* Bode, 1953, *Sunotettigarcta kudryashevae*, *Sanmai*, and *Maculaprosbole* Zheng, Chen and Wang, 2016 from the Jurassic, or the Miocene *Paratettigarcta* Kaulfuss and Moulds, 2015. Cryptic and disruptive colouration are recognized as defense mechanisms for avoiding predation (Quicke 2017), and the fossil record shows that they evolved in Tettigarctidae during much of their history.

3.4.2 Palaeobiogeographical and palaeoclimate considerations

The preservation state of *Maculaferrum blaisi* gen. et sp. nov. does not provide any insight into aspects of tettigarctid biology, such as hair density or feeding apparatus, as in other members of the family (Hamilton 1990; Li *et al.* 2012; Chen *et al.* 2014; Fu *et al.* 2019). However, its

contribution to our understanding of tettigarctid biogeography cannot be overstated. The unique geographical distribution of *Maculaferrum* strongly supports its new genus status based on the anatomical diagnosis outlined above. Tettigarctids were already known to have a global distribution during the Cretaceous ranging from Eurasia to South America, and this discovery finally confirms that their range extended to North America (Fig. 5). The fact that *Maculaferrum* only represents the first occurrence of this family on this continent demonstrates how rare tettigarctids can be in the Cretaceous hemipteran fossil record. Most continents have only one or two known fossils representing this family (Hamilton, 1990; Kaulfuss & Moulds, 2015; Menon, 2005; Nel et al., 1998); they are conspicuously absent from a number of well-sampled Lagerstätten, such as the Jehol biota (Fu *et al.* 2019), Koonwarra (Shcherbakov 2009), or the spatially and temporally close New Jersey amber (Grimaldi *et al.* 2000). In the Lagerstätten that do contain them (such as the Yanliao biota or the Crato Formation (Hamilton 1990; Li *et al.* 2012; Chen *et al.* 2016)), species are only ever represented by one or two specimens, and their occurrence is not clearly correlated with preservation potential. Not a single species was known in the form of amber inclusions until 2019, and these occurrences are all reported from the Hukawng Valley, a single exceptional locality in Myanmar (Fu *et al.* 2019; Jiang *et al.* 2019). In contrast, the only tettigarctids known from Africa and New Zealand, and now North America, consist in isolated fragmentary wings (Kaulfuss & Moulds, 2015; Nel et al., 1998). Taphonomical bias may explain this situation more than any rarity in the Cretaceous biocoenoses since tettigarctids have a life history that would make them less likely to fossilize as part of Lagerstätten than lacustrine or riparian insects.

How does this discovery contribute to our understanding of cicadoid eco-evolutionary trends throughout the Cretaceous? At the time of Moulds' (2018) review of cicadoid diversity, seven tettigarctid species were known from the Early Cretaceous, and none from the Late Cretaceous. One year later, four species (including *Maculaferrum blaisi* gen. et sp. nov.) are known from the Late Cretaceous, from very distant localities (Fig. 5). If the relative dating of the Redmond Formation is accurate, it would be of a similar age to the reasonably constrained Hukawng Valley of Myanmar, the only other locality to have produced other Cenomanian tettigarctids (Shi *et al.* 2012; Fu *et al.* 2019; Jiang *et al.* 2019). These new discoveries suggest that the decline in tettigarctid diversity was not as abrupt as first envisioned. They do not completely refute the hypothesis of competitive displacement by Cicadidae (Wang & Zhang 2009), but suggest a shift

in its timing towards the Cenozoic, or at least nearer the end of the Cretaceous, especially now that *Burmacicada protera* Poinar Jr. and Kritsky, 2012 is assigned to Tettigarctidae instead of Cicadidae (Moulds 2018; Chen et al. 2019a, b). The discovery of *Maculaferrum* also leads us to doubt Fu et al.'s (2019) hypothesis on Southeast Asia as a tropical refuge for tettigarctids during the Cenomanian. It may be supported for more specialized taxa because of their unique occurrence in an environment that is exceptionally humid compared with localities that experienced a more seasonal tropical climate (Spicer *et al.* 1996; Grimaldi *et al.* 2002; Hay & Flögel 2012). However, our discovery demonstrates the occurrence of tettigarctids at a higher latitude that experienced a warm temperate to subtropical climate with a significant seasonality (Demers-Potvin & Larsson 2019), and suggests that the versatility demonstrated by the diverse Jurassic record in this family extended at least into the beginning of the Late Cretaceous. Conversely, it also confirms their presence in another habitat experiencing milder conditions than their extant relatives' current refuge (Claridge *et al.* 1999). Considering the evidence for Mesozoic tettigarctids living in tropical to subtropical environments, this family constitutes yet another example of an insect group for which uniformitarian assumptions based on the natural history of modern species cannot be applied to extinct relatives.

At a higher taxonomical level, the discovery of *Maculaferrum blaisi* gen. et sp. nov. offers more insight on the biogeography of its subfamily. Jurassic taxa assigned to Tettigarctinae were distributed in Europe, as well as central and northeastern areas of Asia (Kazakhstan, Kyrgyzstan and northeastern China) (Martynov 1937; Bode 1953; Hong 1983). In the Early Cretaceous, members of this subfamily are only found in Northern Africa and Eastern South America (Nel *et al.* 1998; Menon 2005). The discovery of *Maculaferrum* extends the Late Cretaceous record Tettigarctinae from the West Burma Block to northern areas of North America. The spatiotemporal distribution of the known fossil record of Tettigarctinae suggests a dispersal of the subfamily over its history in two possible scenarios: either an expansion of the range, or a retreat of the group from warm areas of Europe and/or central and eastern Asia towards equatorial Africa, South America and the West Burma Block, then to slightly cooler areas at higher latitudes during the Cenozoic (Fig. 6). Considering that the North Atlantic Ocean was opening during the Late Cretaceous, the presence of *Eotettigarcta scotica* Zeuner 1944 in the Palaeocene Isle of Mull deposits, Scotland, could be explained by a dispersal across the Thulean Land Bridge, which is considered to have been the most important path of interchange for temperate biota in the earliest span of the Eocene

(Sanmartín *et al.* 2001; Archibald *et al.* 2011). Alternatively, a vicariance hypothesis cannot be ruled out considering that the oldest known tettigarctids existed in Australia likely before the breakup of Pangaea (Lambkin 2019), and that this same landmass is now home to the family's only extant representatives (Moulds 2005). Such a small sample size stretched over a ~200 Ma fossil record may restrict our ability to precisely elucidate the biogeographical patterns of tettigarctids.

3.5 Conclusions

The discovery of *Maculaferrum blaisi* gen. et sp. nov. finally confirms the presence of the once-widespread cicada family Tettigarctidae in North America and contributes to filling a Late Cretaceous gap in the fossil record of hairy cicadas. The erection of a new genus is strongly supported by distinctive forewing venational characters and a unique geographical distribution. This is the most recently described member of Tettigarctinae to display a combination of venational characters supposedly diagnostic of tribes Protabanini, Meunierini and Tettigarctini. Consequently, it supports the hypothesis according to which the definitions of these taxa are based on many convergent or plesiomorphic characters, and that they should be revised accordingly. It also leads us to propose the hypothesis that tettigarctids were still thriving at least at the start of the Late Cretaceous, and that their competitive displacement by singing cicadas occurred at least later than the Cenomanian. Additionally, the relatively high palaeolatitude of the locality of this new genus supports a hypothesis of shifts in the extent of the world distribution of Tettigarctinae throughout the lineage's history. More fossil discoveries are necessary to refine these ecological and biogeographical hypotheses. Together with a more thorough study of wing venation patterns and variability among the extant *Tettigarcta* species, they should also contribute to refining the taxonomy of this family. The small number of known Late Cretaceous, and more precisely Cenomanian, sites means that it remains difficult to determine whether the abundance of rare occurrences in the Redmond entomofauna is caused by taphonomical bias or a biogeographically significant phenomenon. *Maculaferrum* is the first hemipteran described from Labrador's Redmond Formation, and represents the beginning of a renewed scientific interest in this unique and remote Cretaceous locality. Further descriptions of this recently expanded palaeocommunity, and its eventual comparison with the relatively spatially and temporally close assemblage in New Jersey amber, may provide insight on this matter on a more continental scale.

3.6 References

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3.7 Figures

Figure 1. Geographical location and geological setting of the Late Cretaceous (Cenomanian) Redmond Formation. **(A)** Location of the Redmond Formation near Schefferville in Labrador, Canada ($54^{\circ}41'N$, $66^{\circ}45'W$). Exposures of the Sokoman Formation based on Conliffe (2016). **(B)** Prospecting along the spoil pile to the West of the Redmond no.1 mine, where the specimen was discovered. **(C)** South-East facing view of the mine from the top of the western spoil pile. The open-pit mine is now flooded by groundwater.

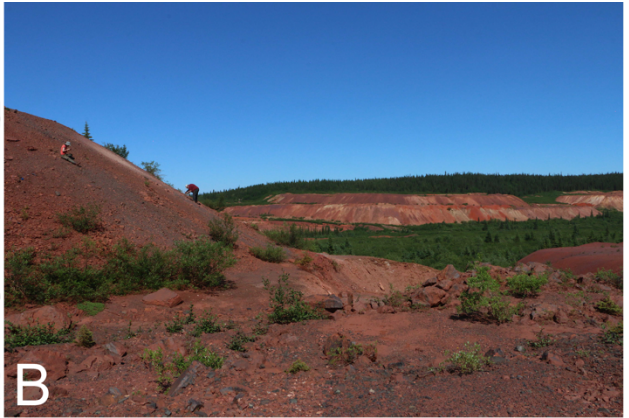
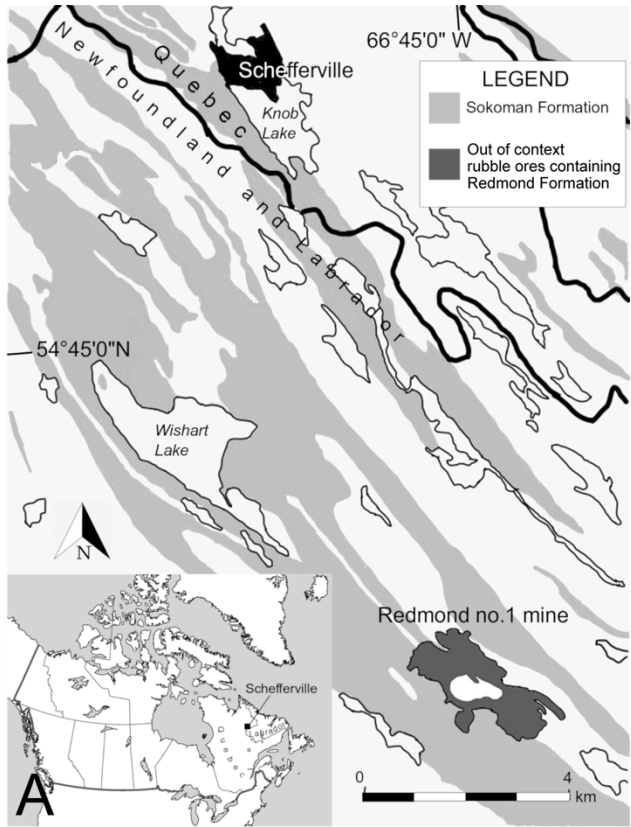
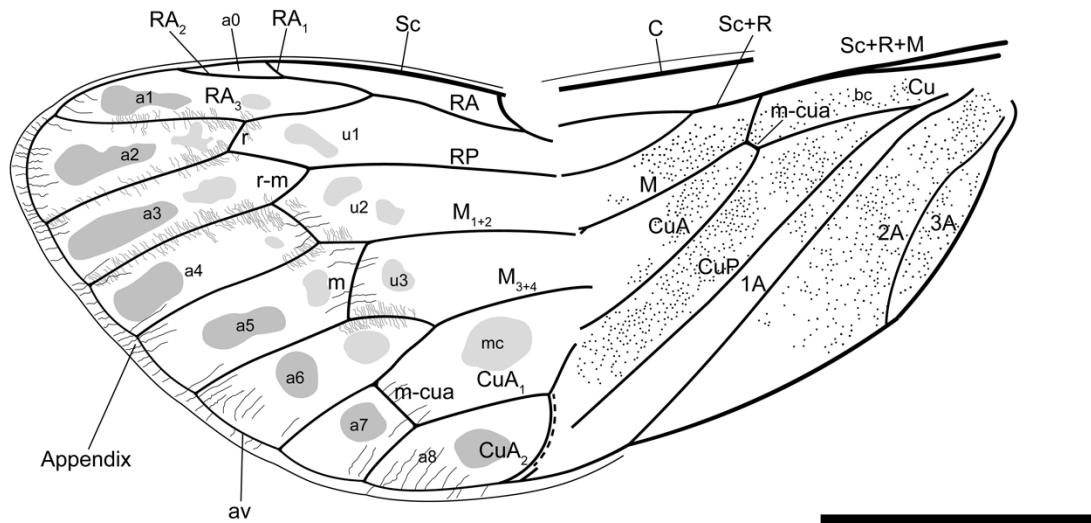


Figure 2. Hairy cicada *Maculaferrum blaisi* gen. et sp. nov., holotype RMIP 2018.18.24 from the Late Cretaceous (Cenomanian) Redmond Formation, Labrador, Canada. **(A)** Habitus photograph extracted from the RTI file (see Supplementary Material). **(B)** Interpretative line drawing of habitus. Wing venation terminology after Moulds (2005). A, anal vein; a, apical cell; av, ambient vein; bc, basal cell; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M_{1+2} , two anterior branches of M; M_{3+4} , two posterior branches of M; m, medial cross vein; mc, medial cell; m-cu, mediocubital cross vein; RA, radius anterior; RP, radius posterior; r, radial cross vein; r-m, radio-medial cross vein; Sc, subcosta; u, ulnar cell. Striae along wing apex represented by black lines. Tubercles along apical vein segments represented by grey lines. Visible portion of nodal line represented as dashed line. Scale bar 5 mm.



A



B

Figure 3. Photomicrographs highlighting specific characters of the forewing of hairy cicada *Maculaferrum blaisi* gen. et sp. nov., holotype (RMIP 2018.18.24) from the Late Cretaceous (Cenomanian) Redmond Formation, Labrador, Canada, extracted from the RTI file (See Supplementary Material). **(A)** Apical portion of the forewing, striae crossing ambient vein either side of apex, under specular enhancement rendering mode. **(B)** Emphasis on the apex, with striae particularly visible on the apicalmost segment of the ambient vein, under specular enhancement rendering mode. **(C)** Longitudinal veins RP, M₁ and M₂; note rows of tubercles emerging perpendicular to veins, under specular enhancement rendering mode. M, media; RP, radius posterior. **(D)** Posteriormost segment of nodal line between CuA₂ and post-burial fracture, running subparallel to both structures. CuA, cubitus anterior. **(E)** Same as in D, under specular enhancement rendering mode. **(F)** Round to oblong patches arranged in a row near apical edge of apical cells. Second row of smaller patches visible in basal part of apical cells. **(G)** Emphasis on part of the pre-nodal area featuring a punctate pattern. Forking point of vein M (into M₁₊₂ and M₃₊₄) highlighted in inset. M, media. **(H)** Interpretative drawing of area highlighted in (G).

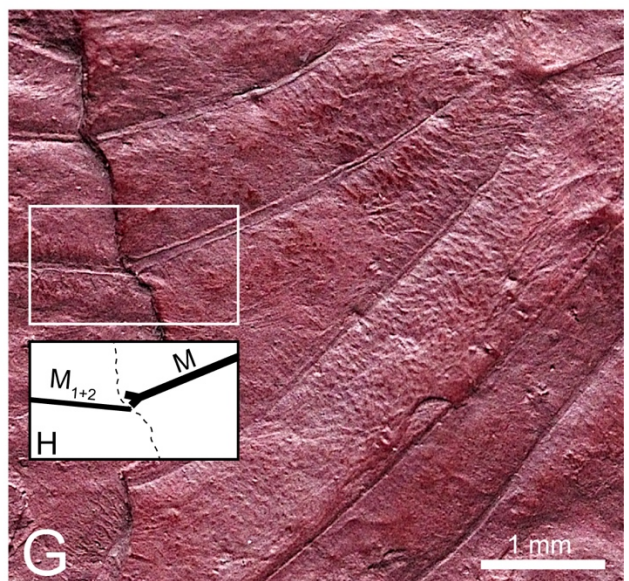
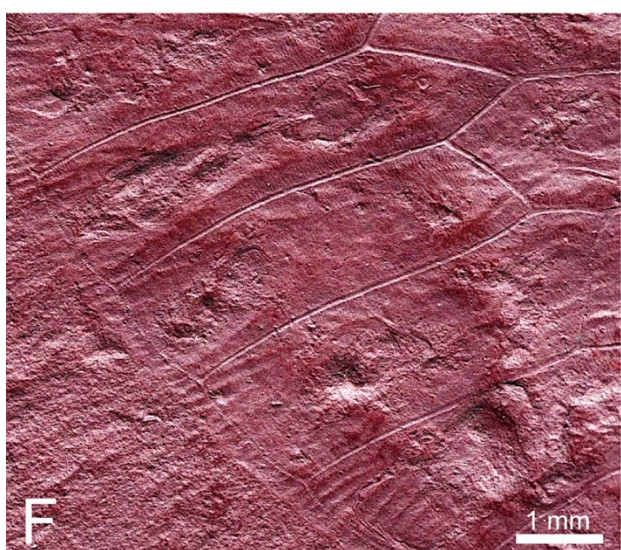
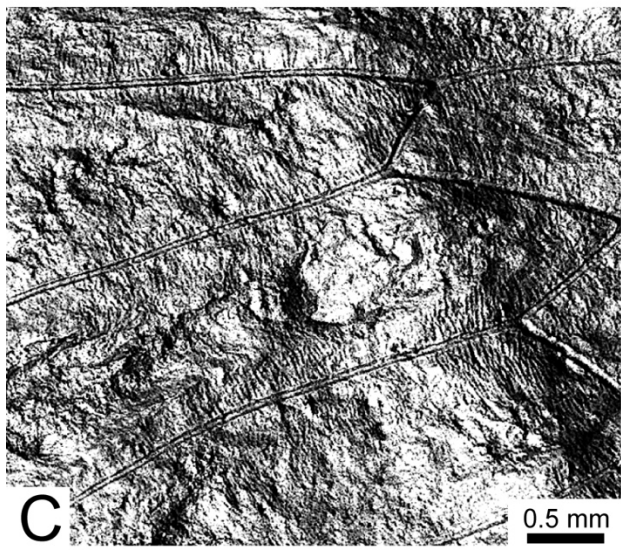
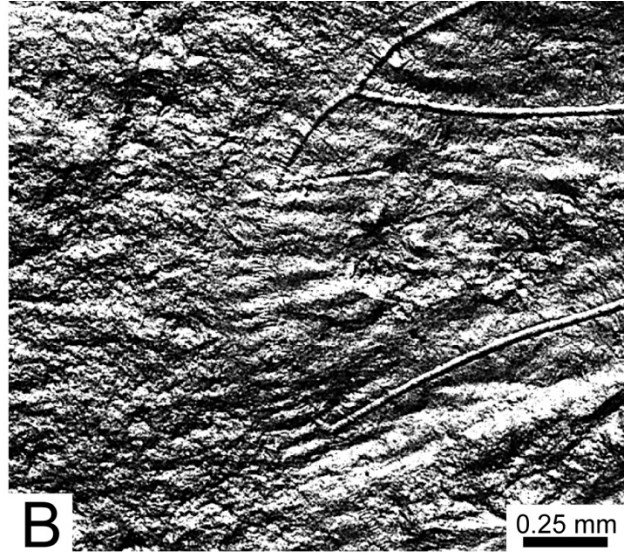
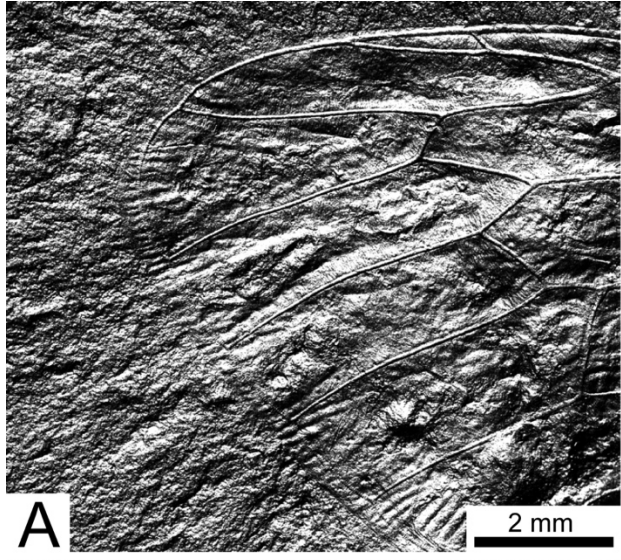


Figure 4. Comparison of hairy cicada *Maculaferrum blaisi* gen. et sp. nov., holotype (RMIP 2018.18.24) from the Late Cretaceous (Cenomanian) Redmond Formation, Labrador, Canada, with forewings of extant relatives. (A) Interpretative drawing of forewing in pre-burial state, based on extant and extinct relatives. (B) Left forewing of male *Tettigarcta crinita* Distant, 1883 from Southern Victoria, Australia (NMV HEM5660), dorsal view. (C) Left forewing of female *Tettigarcta tomentosa* White, 1845 from Tasmania, Australia (NMV HEM476), dorsal view. Note colouration pattern on post-nodal half: round patches near junction of terminal longitudinal veins with ambient vein, a larger darker round patch in cell a2, smaller irregular patches along more basal segments of longitudinal veins, and large oblong to irregular patches along cross veins and short segment of M₁. A, anal vein; a, apical cell; av, ambient vein; bc, basal cell; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M₁₊₂, two anterior branches of M; M₃₊₄, two posterior branches of M; m, medial cross vein; mc, medial cell; m-cu, mediocubital cross vein; RA, radius anterior; RP, radius posterior; r, radial cross vein; r-m, radio-medial cross vein; Sc, subcosta; u, ulnar cell. Scale bars 5 mm.

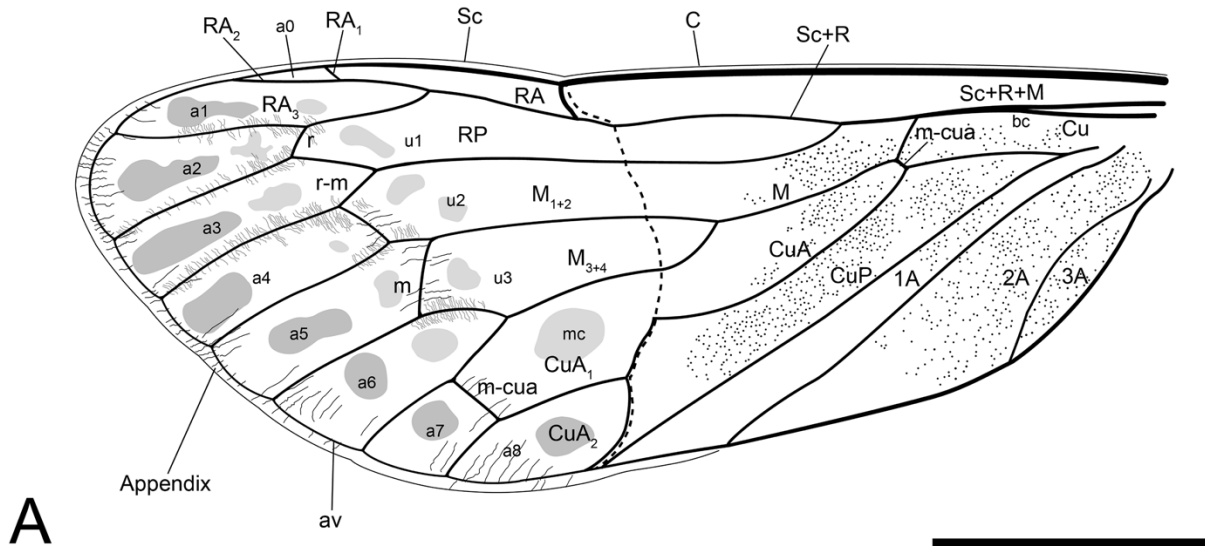


Figure 5. (A) Spatial and geographical distribution of cicadoid occurrences in the Cretaceous compared with extant tettigarctids. Red star represents hairy cicada *Maculaferrum blaisi* gen. et sp. nov., holotype (RMIP 2018.18.24) from the Late Cretaceous (Cenomanian) Redmond Formation, Labrador Canada; black represents occurrences of cicadoid relatives; blue diamonds represent extant species. (B) Habitus photograph of male *Tettigarcta crinita* Distant, 1883 from Southern Victoria, Australia (NMV HEM5660), dorsal view. (C) Habitus photograph of male *Tettigarcta tomentosa* White, 1845 from Tasmania, Australia (NMV HEM472), dorsal view. Scale bars 5 mm.

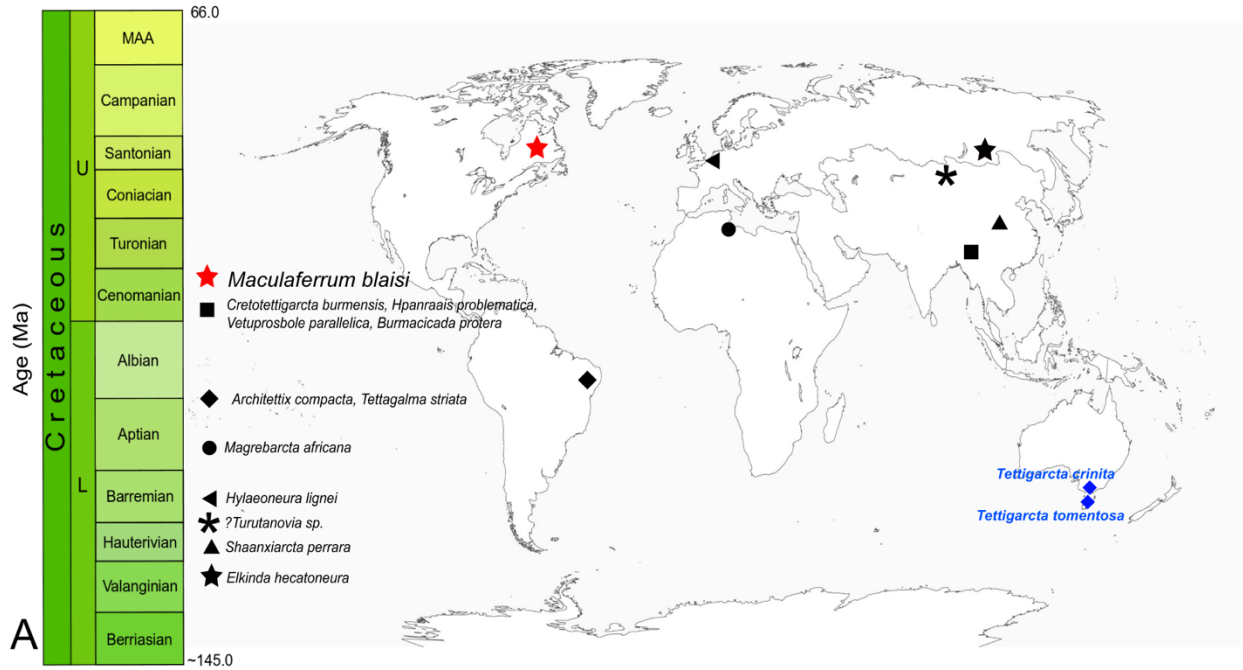
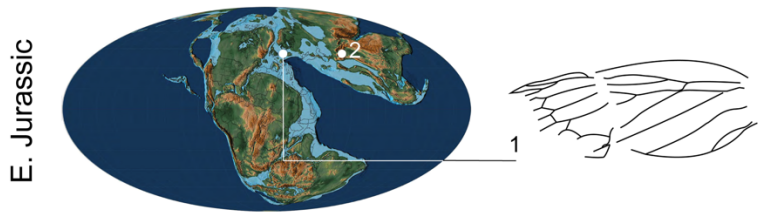
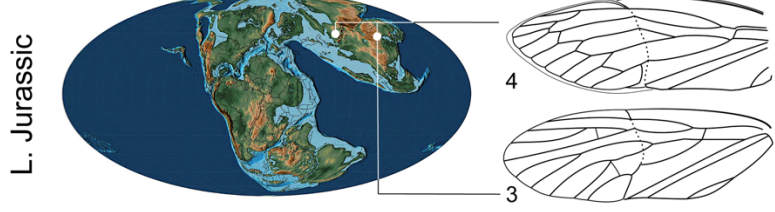
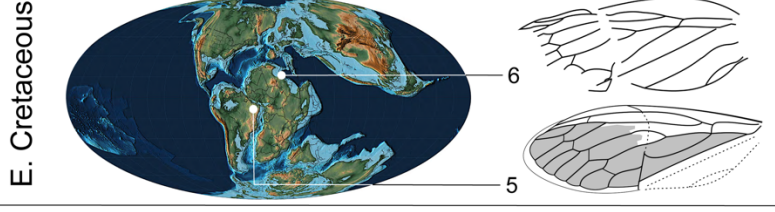
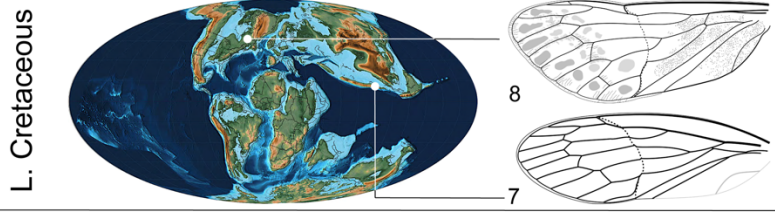
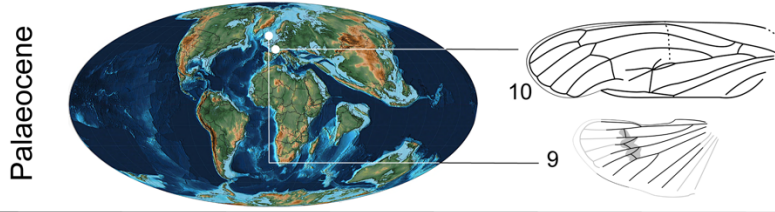
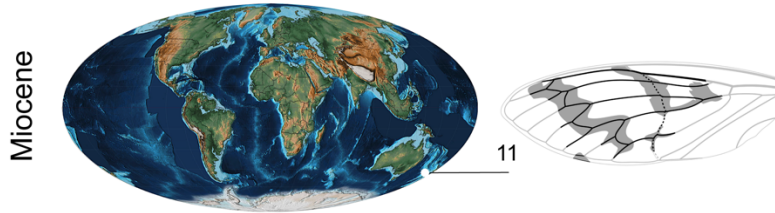
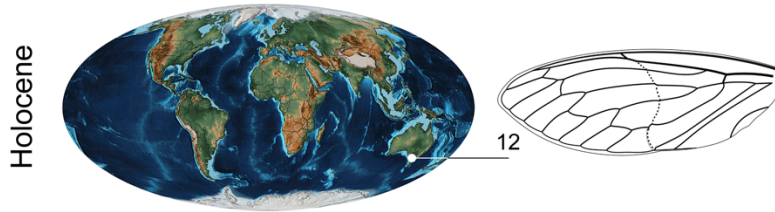


Figure 6. Tettigarctinae occurrences through time. 1 – *Liassocicada antecessens* Bode, 1953 (use of drawing from Nel et al. (1998) for convenience due to poor preservation of original specimen); 2 – *Kisylia psylloides* Martynov, 1937 from Early Jurassic Kisyl-Kiya, Kyrgyzstan (drawing absent due to very poor preservation); 3 – *Protabanus chaoyangensis* Hong, 1982 from the Middle/Late Jurassic (Callovian/Oxfordian) Jiulongshan Formation, China; 4 – *Sunotettigarcta* (represented by drawing of *Sunotettigarcta kudryashevae* Shcherbakov, 2009 from Late Jurassic Karatau, Kazakhstan); 5 – *Tettagalma striata* Menon, 2005 from the Early Cretaceous (Aptian) Crato Formation, Brazil; 6 – *Magrebarcta africana* Nel et al., 1998 from the Early Cretaceous (Aptian) Duriet Formation, Tunisia; 7 – *Cretotettigarcta burmensis* Fu et al., 2019 from the Late Cretaceous (Cenomanian) Hukawng Valley, Myanmar; 8 – *Maculaferrum blaisi* gen. et sp. nov., holotype (RMIP 2018.18.24) from the Late Cretaceous (Cenomanian) Redmond Formation, Labrador, Canada; 9 – *Eotettigarcta scotica* Zeuner, 1944 from the Palaeocene Isle of Mull, UK (only known from a partial hind wing); 10 – *Meuniera haupti* Piton, 1936 from the Palaeocene Menat quarry, France; 11 – *Paratettigarcta zealandica* Kaulfuss and Moulds, 2005 from the Miocene Hindon Maar, New Zealand; 12 – *Tettigarcta crinita* Distant, 1883 from Southern Victoria, Australia (extant). Palaeogeographical maps from Scotese (2001). The classification of *Liassocicada ignota* Brodie, 1845 within Cicadoprosobolinae introduces uncertainty about the affinities of *L. antecessens* to Tettigarctinae (Shcherbakov 2009). Reproduced schematic drawings not to scale; 1, 4, 6, 7, 9, 10 and 11 mirrored to facilitate comparison with *Maculaferrum*. Fossil occurrences retrieved from the Paleobiology Database (Czaplewski 2019).



CHAPTER 4. General discussion and final conclusions

The following chapter discusses in further detail the results presented in the last two chapters. It begins with a more global context for the palaeoclimatic reconstruction of the Redmond environment outlined in Chapter 2. It is followed by a deeper discussion of the implications of the Redmond flora for our understanding of the angiosperm radiation in the Cretaceous, followed by an assessment of the other potential palaeoclimate indicators available from this locality. In light of the hemipteran described in Chapter 3, particular attention is devoted to the potential of fossil insects as palaeoclimate indicators.

4.1 The Redmond Formation in the Cretaceous hothouse

Over a period ranging from 1976 to 2005, Schefferville has had a mean annual temperature of -4.7°C , with a maximum mean monthly temperature of 12.4°C in July and a minimum mean monthly temperature of -23.4°C in January (2017). Over the same period, it has had a mean annual precipitation of 810 mm, and 2,978 freezing degree-days per year. This climatic data situates the region in zone Dfc (snow climate, fully humid, cool summer) in the Köppen-Geiger Climate Classification (Kottek *et al.* 2006). The quantitative climate estimate performed in Chapter 2 on the best-preserved angiosperm leaves of the Redmond Formation confirms that the region surrounding Schefferville had a far milder mesothermal climate. The mean annual temperature (MAT) in this part of the Quebec/Labrador Peninsula would have been $\sim 15^{\circ}\text{C}$, approximately equivalent to modern global averages. However, it would have been much lower than the Cenomanian global average (Hay & Flögel 2012). Looking at temperature estimates for the same palaeolatitude as the Redmond ecosystem ($\sim 50^{\circ}\text{N}$), the MAT of this locality falls $\sim 3^{\circ}\text{C}$ below the value for the most conservative palaeolatitudinal temperature gradient (Hay & Flögel 2012). Considering that the data for these models is derived from sea-surface temperature, and that the Redmond ecosystem was already located far inland at that time, the effect of continentality may contribute to this discrepancy.

Despite this relatively low temperature estimate, it does not yet constitute a case of a continental interior paradox, in which temperatures predicted from General Circulation Models (GCMs) are significantly lower than those suggested by fossil or sedimentological proxies (DeConto *et al.* 1999). Although eastern Canada had an extensive area inland, its climate

discrepancies between these different methods were not as important as in other regions such as Eastern Russia (Spicer 2003; Spicer *et al.* 2008). Instead, my results, obtained largely from palaeobotanical evidence, generally agree with local and regional GCM predictions (Sellwood & Valdes 2006; Fluteau *et al.* 2007; Hay *et al.* 2018). Recent additions to the flora do not change its interpretation as part of the northern mid-latitude warm humid belt (Chumakov *et al.* 1995), since its composition remains very similar to that of Cenomanian floras from the Dakota Formation (Upchurch & Dilcher 1990; Wang & Dilcher 2018). Among coeval North American floras that have been studied with CLAMP, those from the Dakota Formation (such as Rose Creek) unsurprisingly have the most similar temperature parameters (see Chapter 2; Table 3). Differences in predicted climate results between the Redmond and Dakota floras are probably explained by different frequencies in similar leaf morphotypes. Since there is no evidence of significant palaeoelevation differences between northern Appalachia and the eastern shore of the Western Interior Seaway, the lower palaeolatitude for all Dakota sites may explain their slightly longer estimated growing season.

4.2. Limitations of current palaeoclimate indicators for the Redmond Formation

4.2.1 How woody were angiosperms in the Cenomanian?

The foundations of CLAMP upon principles of natural selection explaining phenotypic variability in leaf characters largely contribute to its robustness as a climate inference method. It has also shown to be robust to taphonomical loss that inevitably affects the fossilization of an extinct community. Experiments on extant floras demonstrate that uncertainties caused by taphonomical loss (either of diversity or of specific leaf characters) are not significantly different from statistical CLAMP uncertainties (Spicer *et al.* 2011), and that CLAMP estimates derived from leaf litter (a fraction of standing vegetation diversity) do not differ significantly from meteorological data (Dilcher *et al.* 2009).

Statistics aside, uncertainties remain about the influence of streamside and lakeside environments on this leaf-climate relationship, and these are precisely the most favourable terrestrial depositional settings for fossilization (Behrensmeyer & Hook 1992). Lake assemblages have been shown to contain an unexpectedly high proportion of small leaves, which would lead to underestimates in temperature and precipitation (Stranks 1996). These habitats (which often have more disturbed conditions than dry land) also seem to contain an unexpectedly high proportion of

leaves with toothed margins belonging to early successional species or vines or lianas, which could lead to underestimates of 2.5 – 5°C for extinct ecosystems (Wolfe & Upchurch 1987; Burnham *et al.* 2001; Kowalski & Dilcher 2003). Similarly, disparities between CLAMP temperature estimates and meteorological data seem influenced by subcanopy microclimates and a proximity to water bodies more than character or diversity loss in the leaf litter (Spicer *et al.* 2011). Such confounding factors are sufficiently high to misinterpret the past climate of an entire region.

Cretaceous floras have an additional confounding factor because the identification of the source plant of many fossil leaf morphotypes remains debatable, meaning that it is unclear whether some leaves belonged to woody or non woody dicotyledons (such as the aforementioned lianas). Most of the Early Cretaceous and Cenomanian wood samples from Europe have thin-walled cells, with inconsistent vessel sizes and distribution (Philippe *et al.* 2008). These characteristics suggest these trees had a high vulnerability to embolism and far less robust trunks than more derived relatives (Carlquist 1977), but that they would have been capable of very rapid growth (Wheeler & Baas 1991). Such adaptations are expected of plants that lived in disturbed depositional settings, which are widely accepted as the habitat in which angiosperms first evolved (Doyle & Hickey 1976; Retallack & Dilcher 1986; Royer *et al.* 2010). However, they are not necessarily characteristic of large angiosperm trees.

This is a problem since leaves belonging to woody dicots (preferably trees) are the only structures to present a consistent and quantifiable response to environmental change (Wolfe 1993; Spicer 2006; Li *et al.* 2016). There are two main hypotheses on the timing of the ecological diversification of woody angiosperms, more precisely on the timing of their colonization of more stable habitats at the expense of gymnosperms and pteridophytes.

The most widely accepted hypothesis situates this turnover during the Albian-Cenomanian transition, which coincides with a sharp rise in angiosperm species richness: it is in the Cenomanian that angiosperms reach 70% of plant diversity and that the first modern families appear (Wing & Boucher 1998; Lupia *et al.* 2000). As shown in the European plant fossil record of that transition, the frequency of angiosperm remains increases substantially in inland settings close to fresh water, leading to an occupation of most terrestrial depositional environments (Coiffard *et al.* 2012). More precisely, the wood record shows a sevenfold increase in angiosperm wood generic diversity (Philippe *et al.* 2008).

It is also a time of structural innovations, such as increased photosynthetic capacity due to a more complex and regular leaf venation architecture, and increased wood hydraulic efficiency, both of which are key adaptations of large broad-leaved trees (Feild *et al.* 2011). A gradual increase in vein complexity can be observed in the Potomac Group on the Eastern seaboard, a continuous sequence spanning almost the entire radiation of early angiosperms from the Aptian to the Cenomanian (Doyle & Hickey 1976; Hickey & Doyle 1977). Leaves from the Aptian-early Albian Patuxent and Arundel formations are generally small, and their venation pattern is highly irregular with little bilateral symmetry. Those found in the middle to late Albian Patapsco Formation increase in size, diversity and venation complexity, with the appearance of peltate and ovate-cordate morphotypes and pinnately compound leaves. However, their disturbed streamside depositional environments and leaf economic traits, such as low leaf mass per area correlated with a short lifespan and a narrow petiole (Royer *et al.* 2007), suggest they remain early successional ruderals (Royer *et al.* 2010). This trend culminates in the Cenomanian Raritan Formation, which has an abundance of palmately lobed and palinactinodromous leaves with a more regular venation pattern, although they remain restricted to the same depositional environment (Hickey & Doyle 1977, Fig. 68). Of 169 identified angiosperm species, the Raritan Formation contains 131 angiosperms (Dorf 1952).

Another hypothesis situates this turnover in vegetal niche occupation much later: it proposes that angiosperms remained ruderal herbs or small trees with early successional strategies and little competitive ability at least as late as the Campanian, while ferns and gymnosperms remained largely dominant in more stable or stressed environments (Wing & Boucher 1998). After all, a high diversity within a given taxon does not necessarily imply a higher variety of ecological niches (Wing & Sues 1992). This hypothesis is supported by the depositional environments of the North American palaeobotanical record. Contrary to the European record, ferns and conifers still dominated inland soils (whether well drained or swamp settings) in abundance throughout much of the Late Cretaceous, while angiosperms remained restricted to channel and other disturbed settings (Retallack & Dilcher 1986). It is also supported by the cell structure of most Cretaceous woods that seems to indicate less solidity but a faster growth rate in agreement with a lifestyle as ‘weedy trees’ in a disturbed environment. Following this interpretation, the high wood hydraulic efficiency would be an adaptation to fast growth rather than to increased biomass. According to this hypothesis, the acquisition of derived leaf characters in the Cenomanian does not necessarily

mean that angiosperms had already evolved the entire modern suite of growth architecture and life history strategies (Philippe *et al.* 2008; Wheeler & Lehman 2009).

Dorf's (1959) Cenomanian age estimate for the Redmond flora is based on morphological similarities of its angiosperm leaves to those of the Raritan and Dakota floras (Newberry & Hollick 1886; Lesquereux 1892; Berry 1910). For instance, the occurrence of *Cissites platanoidea* (and its high relative abundance in the Redmond flora) seems a particularly strong indicator of a Cenomanian age since it is not found in other ages (Lesquereux 1892; see Chapter 2). The Cenomanian is considered to be the earliest stage in which all major dicotyledonous leaf morphotypes existed, and many of the leaves in the Redmond flora are very similar to modern woody angiosperm genera such as *Platanus*, *Sassafras*, *Magnolia* and *Sterculia* (see Chapter 2). The relative dating of this community seems to support the first hypothesis according to which angiosperms occupied most of their modern ecological niches by the start of the Late Cretaceous. It gained further credence with the discovery of a silicified log in the Turonian Mancos Shale (~92 Ma) that had a maximum preserved diameter of 1.8 m, which could equate to an estimated height of 50 m (Jud *et al.* 2018). Being the largest known angiosperm preceding the Campanian, and the earliest case of an angiosperm tree with a diameter exceeding 1 m, it suggests that some woody angiosperms were definitely part of the forest canopy at the start of the Late Cretaceous. It suggests that many of the leaves in the Redmond flora could have belonged to canopy trees, yet still it does not determine the exact ecological niche of their source plants.

Bearing these concerns in mind, the major uniformitarian assumption of CLAMP (according to which the relationship between woody angiosperm leaves and ambient climate has not changed for ~100 Ma) has been tested with Campanian and Cenomanian floras by plotting their respective palaeolatitude (with which MAT has a negative relationship established by extraneous evidence from oxygen isotopes) against their respective frequency of leaves with untoothed margins (Spicer 2003, fig.4.61). The high similarity between the gradients for these two stages shows that the relationship to climate was similar between Cenomanian woody dicot floras and Campanian ones (some of which definitely had an ecological diversity comparable to extant floras). In agreement with Wolfe (1993), it also shows that leaf margin type at least is not significantly affected by temporal variations in CO₂ concentration. Nonetheless, more work needs to be done on the identification of possible tree leaves in the Redmond assemblage and elsewhere, and on the life history traits of these first angiosperm trees. Only then can CLAMP be applied

further, as in a study on Miocene (Tortonian) macrofloras from California where estimated warm month mean temperature and relative humidity were used to calculate the probability of ignition, offering insight into the region's past fire regimes (Boulton & Belcher 2019).

If this method can be tested for older floras, it could be used to corroborate evidence from globally abundant Cretaceous charcoal remains suggesting that this period had far more intense fire regimes due to higher temperatures and O₂ concentrations, as well as many climatic zones with a dry season (Bond & Scott 2010). Considering that angiosperms have a higher productivity than gymnosperms, that their litter is more easily decomposed and that they accumulate flammable biomass more rapidly, they could have thrived under intense fire disturbance, leading to a positive feedback between their eventual radiation and the initiation of new fire regimes (Berendse & Scheffer 2009; Bond & Scott 2010). In turn, this shift in ecosystem dynamics could be a major abiotic factor in the decisive phase of the radiation of flowering plants during the Albian-Cenomanian transition.

4.2.2 *Alternative palaeoclimate indicators for the Redmond Ecosystem*

The time limitations of this project led me to select the most appropriate palaeoclimate proxy for the palaeoecological questions that were addressed on the Redmond community. In this respect, fossil angiosperm macrofloras are particularly valuable since they demonstrate a very high sensitivity to local and regional climate conditions while also providing biological information on community structure and interactions (Bamforth *et al.* 2014). Nevertheless, the credibility of this palaeoclimate reconstruction will vastly increase if the CLAMP results can be cross-checked by results from at least one other independent climate proxy. Despite their high precision and accuracy for estimating sea surface temperature, oxygen isotopes derived from foraminifera cannot be directly compared with results found in the Redmond Formation's rock record (Spicer 2003), since this locality was already far inland in the Cretaceous (Scotese 2001).

Climate-sensitive rocks from the Redmond Formation are already known: Blais (1959) recognized the lateritic origin of the argillite, and the same deposit is indicated to contain kaolinite on a map of Albian-Turonian lithological climate indicators (Boucot *et al.* 2013). Despite the congruence between their occurrence and the CLAMP results obtained in this study, an updated clay weathering analysis is recommended (Velde & Meunier 2008). In sites lacking geological context, where fossils are recovered from float and do not seem to contain biogenic oxygen, it is

usually the only available method for cross-checking results from leaf physiognomy (Arens & Harris 2015). Coal fragments (no more than 4 cm³) have also been found among the rubble piles during the 2018 field season, although the lack of geological context renders their age of deposition uncertain.

The increase in the abundance of non-angiosperm plant fossils known from the site raises the possibility of a bioclimatic analysis (BA) as one of the only available quantitative alternatives to CLAMP. The latest fieldwork has led to the discovery of more fern and conifer taxa, but they must be identified before being included in such a study (see Chapter 2). Some of the better-preserved specimens can be attributed to the pinaceous conifer *Abietites longifolius*, already identified by Hickey in the first historical collection from the site (see Chapter 2, Fig. 2C), and conifers such as *Pinus* and the cupressaceous *Sequoia* and *Widdringtonites* (Armstrong 1993). BA has been used successfully as a complement to taxon-independent methods such as CLAMP and LMA (Greenwood *et al.* 2005; Fletcher *et al.* 2014; Stults & Axsmith 2015), and has the potential advantage of including a wider diversity of the local plant community. However, the major limitations of such a taxon-based inference, especially for such an old flora, must still be considered (see Chapter 1).

The samples collected from the Redmond site over the 2013 and 2018 expeditions have yet to be inspected for spore or pollen traces. In a report to the Geological Survey of Canada (Office Report No. F1-4-1965-DCM), Glenn E. Rouse recognized 8 angiosperm genera, 3 conifers, 2 ferns and one dinoflagellate in samples extracted from the Ruth Lake deposit (Rice 1969). The estimated age for this palynoflora ranged from latest Cretaceous to Palaeocene, which vastly contradicts the relative dating of the Redmond argillites based on the insects and macroflora. Considering the limitations of palynological studies at deep time scales (see Chapter 1), it can mean two things: either the rubble ores around the Ruth Lake mine were deposited during a later or longer period than the time of deposition of the Redmond argillites, or the sampling and identification biases are too high to produce a meaningful result even if the rubble ores were indeed of the same age as the fossil-bearing argillite. This result sheds further uncertainty on the age of the lignified tree trunks from Ruth Lake, one of which had a diameter of at least 1 m (pers. obs.). Their large size and the taxonomic affinity to *Cuppressinoxylon* already suggest that these trees thrived in a far milder climate than the present conditions (Usher 1953; Blais 1959). Even if their relative dating could be refined to prove a Cenomanian age, the cell structure of most specimens is too deteriorated to

be studied. A similar case comes from the Potomac Group, where isolated lignite logs with thick and dense annual growth rings have been reported among clay beds containing a diverse macroflora (Fontaine 1889). However, their silicification state raised the possibility that they had been deposited at an earlier age and subsequently reworked into younger sediments.

4.2.3 *Insects as potential palaeoclimate indicators*

The Redmond Formation may be lacking in alternative climate proxies such as wood, spores or biogenic markers. The latest expedition to this site has demonstrated that it is not lacking in insect impression fossils. Since insects are generally more dependent on local environmental conditions and vegetation than larger (especially endothermic) animals, they have often been used as environmental indicators (Lister & Garcia 2018; Sánchez-Bayo & Wyckhuys 2019). The discovery of gigantic cercopoids in Eocene rocks of the Florissant fossil beds and Okanagan Valley, whose closest extant relatives are now restricted to the Neotropics (Scudder 1890), led to one of the first of these applications. These analyses can even offer insight on the biogeography of a taxon, as shown in the discovery of the first giant formicini ants for the Western hemisphere in the Green River Formation (Archibald *et al.* 2011). Since seven of the eight large modern ant species are restricted to megathermal environments where the mean annual temperature is higher than 20°C, it was inferred that the dispersal of these formicines from Europe to North America across relatively close Arctic landmasses would only have been possible during a hyperthermal event such as the PETM (Archibald *et al.* 2011).

As has been demonstrated in Chapter 1, the major weakness with the use of insects for inferring climatic conditions is that it relies on Nearest Living Relative (NLR) assumptions (Wing & Greenwood 1993). Even if a given fossil insect does belong to an extant family, it cannot be assumed that all members of that family had similar environmental preferences over its entire history, especially if that family has existed for a long span of geological time (Damuth 1992). If a taxon had similar climate tolerances over this time span, the NLR method will provide useful results. This may be the case for termites, which have always been found in tropical to warm temperate ecosystems since their origin, and which are currently absent above 45° on either hemisphere (Eggleton 2000). This is one of the insect taxa that can definitely be described as thermophilic, and whose occurrence in the Redmond Formation in the form of *Cretatermes*

carpenteri Emerson, 1967 does offer a reliable climatic signal. Crucially, it concurs with the quantitative climate estimate now produced for this locality (see Chapter 2).

Alternatively, NLR assumptions will not work for insect families that have shifted their climatic tolerances over their history. The occurrence of a tettigarctid cicada in the Redmond Formation of Cenomanian Labrador is a case in point: it existed at a time when this family had a global geographical range that encompassed multiple climatic zones, but the only two remaining extant species of that family are restricted to cool temperate habitats on a single continent (see Chapter 3). Another example from the Redmond Formation is the occurrence of the alloraphidiid raphidiopteran *Alloraphidia dorfi* Carpenter, 1967. Extant raphidiopteran families require a period of near-freezing temperatures to complete development, which restricts them to temperate habitats (Grimaldi & Engel 2005). However, climate estimates based on extraneous evidence from various Cretaceous localities (including Brazil, Myanmar, New Jersey and now Cenomanian Labrador), show that older raphidiopterans clearly tolerated much higher temperatures (Oswald 1990; Grimaldi 2000; Engel 2002). As a final example, the antlion *Palaeoleon ferrogeneticus* Rice, 1969 lived at a time when its clade (Myrmeleontiformia) was thriving in tropical to warm temperate forests, as opposed to a preference for arid environments in modern times (Badano *et al.* 2018).

These limitations mean that the climate signal from insects must ideally be corroborated by data from independent sources, such as fossil leaves and wood. For instance, studies of Eocene ecosystems from British Columbia's Okanagan Valley show a combination of thermophilic and temperate plants and insects, which is similar to tropical mountainous regions with a cool mean annual temperature but a low seasonality in temperature (Greenwood *et al.* 2005). Minor contradictions between different proxies are often starker at the local scale, as is shown in the Eocene Okanagan site of Quilchena (Archibald & Mathewes 2000). It must be noted that these studies have used bioclimatic analysis instead of the CLAMP method that has been used for the latest palaeoclimate estimate for the Redmond Formation. This means that the climate signal derived from insects may indicate at best a minimum quantitative temperature threshold with a hint of seasonality, which may not offer sufficiently informative comparisons with CLAMP results that quantify a variety of temperature, precipitation and seasonality parameters at a relatively high precision.

4.3 Final conclusions and research implications

This thesis signals a renewed scientific interest in the Redmond Formation, the only Mesozoic sedimentary unit known from the Quebec-Labrador Peninsula, and currently the most biodiverse Mesozoic locality known from Eastern Canada. The first objective of this thesis has been fulfilled, since it contains an updated palaeoclimate estimate based on a recently expanded macroflora, which is composed of quantitative temperature, precipitation and growing season parameters that can be directly compared with results from other fossil floras across the Cenomanian world. Its second objective has also been partially fulfilled, since it contains the first insect description from the Redmond Formation in 50 years (Ponomarenko 1969; Rice 1969), and the palaeoclimate work presents the discovery of new leaf morphotypes for this site. Descriptions of two more new insect species are underway as this thesis is nearing its conclusion. These are only the first steps leading to a more systematic palaeoecological description of this geologically remote extinct ecosystem. In this respect, the overarching objective of integrating the Redmond ecosystem with the help of an expanded fossil record into our current picture of world in the middle of the Cretaceous has been achieved.

As in any other fossil assemblage influenced by taphonomic loss and bias, a further study of the palaeoecology of the Redmond Formation should focus on the site's strengths, *i.e.* the high preservation level of its flora and entomofauna, while minimizing the reliance on its limitations, *i.e.* its current lack of geological context. Studies aimed at understanding community structure further based on leaf economic traits and the lacustrine depositional environment have been suggested in Chapter 2, yet fundamental work remains to be done on the systematic documentation of the biodiversity represented in this fossil assemblage. While the palaeoclimate analysis has required the identification of a moderate number of leaf morphotypes, a taxonomic classification is definitely needed to have a clearer idea of the site's biodiversity and to compare it with that of coeval floras. Concerning insects, more than 570 impression fossils of various completeness and articulation levels were collected during the four weeks of the 2018 expedition to the Redmond no.1 mine. Most identifiable insect specimens are semi-complete isolated wings in a similar preservation state to the tettigarctid described in Chapter 3, which may render the site suitable to an alpha taxonomic diversity estimate at least (Labandeira 2018).

The shallow depth of the original Redmond lake bed indicates a high temporal resolution (as discussed in Chapter 2). Considering that most individual lakes exist over timescales of 10^0 -

10⁴ years (Behrensmeyer & Hook, 1992, table 2.8; A. S. Cohen, 2003), a biodiversity study of this site would fall comfortably within the short term in geological time (defined as <10⁶ years (Labandeira, 2018, table 24.1)). A sufficiently high abundance and diversity of described plants and insects would expand the window that has already been opened with this work on a poorly known region of the Cretaceous world, at a very high spatial and temporal resolution. Since the Redmond fauna is one of the few fossil insect assemblages known from Appalachia and already contains a high proportion of rare taxa in its described record, it could offer unique insight on North American insect biogeography. So far, the only significantly diverse entomofauna known from Appalachia is preserved as amber inclusions and rarer fusainized remains in a few New Jersey sites of Turonian age (Grimaldi *et al.* 2000), but the Redmond entomofauna would represent the Cenomanian on its own for this part of the world.

A holistic approach to studying the plant and insect diversity of the Redmond Formation could be based on the detection of insect ichnofossils on leaves, whether they consist in traces of hole and margin feeding, galling, piercing, sucking, or mining damage (Labandeira & Currano 2013). In extant communities, the number of damage types has been demonstrated to have a strong positive correlation with observed herbivorous insect diversity (Carvalho *et al.* 2014). This additional source of ecological and functional diversity can alleviate the taphonomical bias favouring amber localities by adding data from sites where direct insect fossil evidence is rare (Labandeira 2005). At first glance, the leaves preserved in the Redmond Formation look relatively pristine compared with those of other more diverse localities where plant-insect associations on fossil leaves have been studied (Currano *et al.* 2008; Labandeira *et al.* 1994; Labandeira *et al.* 2002). If some traces of herbivory can be detected in a more detailed study, they could reveal feeding guilds that are not currently represented in the fossil assemblage. This additional insight on ecological and functional diversity could then be joined to the taxonomic diversity data collected from direct fossil evidence. Redmond leaf damage could also be compared with approximately coeval ichnofossils from the Dakota Formation that show that lepidopterans already mined woody dicot leaves 97 Ma, very soon after their appearance (Labandeira *et al.* 1994).

Ecological diversity detected in insect herbivory on leaves also has environmental implications. On a longer time scale than is currently available for Cretaceous Eastern Canada, such ichnofossils have been used to assess the health of terrestrial ecosystems after dramatic disturbances such as the K-Pg extinction (Labandeira *et al.* 2002; Wappler *et al.* 2009). Other

studies suggest that insect feeding activity responds to climate change. Examinations of insect damage on fossil leaves from Wyoming's Bighorn Basin spanning either side of the PETM show that the amount and diversity of feeding traces are both positively correlated with the rise in mean annual temperature (MAT) and pCO₂ that occurs at this time (Currano *et al.* 2008, 2010). Such studies based on a relatively complete fossil dataset may be very relevant to the present anthropogenic biodiversity crisis (Sánchez-Bayo & Wyckhuys 2019).

I hope that this modest work on the extinct community preserved in the Redmond Formation of Cenomanian Labrador leads to an expanded research project. Naturally, one site will never settle the debate on the respective influence of the Red Queen and Court Jester hypotheses on the Cretaceous Terrestrial Revolution on its own. At the moment, the formation is too spatially or temporally constrained to provide any information on the definite causes of the occurrence of a diverse angiosperm flora far inland at such an early time, whether it grew under more benign climatic conditions than in the surrounding territory or whether its spread was facilitated by interactions with insects (of which we still know very little).

What is more certain at this point in time is that the Redmond assemblage contributes to our view of the world in the middle of the Cretaceous by offering a unique window into the evolution of terrestrial ecosystems in Eastern Canada at this pivotal time. The latest studies compiled in this thesis have already significantly expanded our knowledge on this remote locality and fill a gap in our interpretation of palaeolatitudinal gradients through a major hothouse event. Together, they lay the groundwork for interpreting the diversity estimates that will arise from yet more insect impression fossils awaiting a formal description. It is difficult to estimate the proportion of the original lake bed that was exposed on the float surrounding the abandoned Redmond no.1 mine, and thus available for surface collecting during the last field seasons on the site. Bearing this in mind, a sustained effort should be made to explore inside the float in the hope of recovering more remains of this highly restricted sedimentary unit. We may yet have found only a fraction of the plant and animal life preserved in this site in the middle of the Canadian Shield.

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