Mid Paleocene fossil floras and climate from western Scotland

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Declaration of Authorship

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Dedicated to the memory of Dennis Poulter, my grandfather and greatest scientific supporter

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Abstract

Fossil plants of Paleocene age (62 to 59.7 Ma) are preserved within lava sequences in the Hebrides and Northern Ireland. These lavas, collectively referred to as the British Tertiary Volcanic Group (BTVP), were formed due to rifting in the North Atlantic. The fossil floras represent forests that grew between the lavas in periods of quiescence, during which fluvio-lacustrine environments developed on the lava surfaces. The fossil plants provide information on the composition of the Paleocene vegetation and the climate during that interval.

New collections of fossil plants have been made from the Isle of Skye and other collections from Ardtun on Mull were studied. The Allt Mor locality on Skye (60.16 ± 0.45 Ma) has provided the majority of the specimens for this study and represents a pond deposit where broadleaved angiosperm and conifer leaves accumulated. Fourteen angiosperm morphotypes have been identified, many of which show similarities to modern families, including the Platanaceae, Cercidiphyllaceae, Betulaceae, Fagaceae, Juglandaceae, Vitaceae, Cornaceae and Trochodendraceae. Conifer fossils include three ovulate cone types and eight shoot morphotypes attributed to the Cupressaceae and Pinaceae. The Allt Mor assemblage indicates that mixed coniferous forests developed within a palaeovalley, with the vegetation fringing the valley sides and colonising the floodplains of the valley floor. The vegetation of Allt Mor was dominated by climax conifers similar to *Metasequoia*, *Sequoia*, *Chamaecyparis* and *Thuja*. Broadleaved angiosperms such as *Platanites*, *Trochodendroides*, *Corylites* and "*Platycarya* cf" dominated the riparian margins and formed an understory of trees and shrubs in the conifer forests. Comparison with Paleocene floras from other Northern Hemisphere localities indicates that the floras of Skye are most similar to those of the Arctic, particularly those of Svalbard, Greenland and Canada, and were thus part of the Arcto-Tertiary floras of the northern high latitudes.

Palaeoclimate estimates derived from the fossil angiosperm leaves indicate that the climate of Skye had a mean annual temperature (MAT) of ~5°C to 9 °C, was seasonal with warm summers (warm month mean 19.0°C to 25.8°C) and cool to cold winters (cold month mean -3.0°C to 4.2°C). Comparisons with the flora of Ardtun on Mull (60.5 ± 0.3 Ma) reveal that, although these floras share many of the same taxa, the flora is different, with angiosperms dominant, and the conifers that are common in the Allt Mor assemblage are rare or absent. The Ardtun flora also contains thermophilic plants such as *Camptodromites major*, *C. multinervatus* and *Amentotaxus gladifolia*, which are not present on Skye. Palaeoclimate data from these fossil plants indicate significant cooling during the mid-Paleocene, confirmed by other marine and terrestrial proxies, marking a cool climate phase in the middle of the otherwise globally warm Paleocene climate.

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Abbreviations

NAIP	North Atlantic Igneous Province
BTVP	British Tertiary Volcanic Province
Ma	Million years ago
AM	Angiosperm morphotype
OC	Ovulate cone type .
CM	Conifer shoot morphotype
LMA	Leaf Margin Analysis
CLAMP	Climate Leaf Analysis Multivariate Program
MLR	Multiple Linear Regression Model
MAT	Mean Annual Temperature (°C)
CMM	Cold Mean Month Temperature (°C)
WMM	Warm Mean Month Temperature (°C)
GSP	Growing Season Precipitation (mm)
MAP	Mean Annual Precipitation (mm)
3WET	Three wet month mean precipitation (mm)
3DRY	Three dry month mean precipitation (mm)
GSL	Growing Season Length (months)
MART	Mean Annual Range in Temperature (°C)
K/Pg	Cretaceous/Paleogene boundary
LDE	Late Danian Event
ELPE	Early Late Paleocene Event
PETM	Paleocene/Eocene Thermal Maximum

Chapter 1: Introduction

1.1 Introduction

Fossil plants of Paleocene age from the Hebrides and Northern Ireland have been known for over a century. They are present within sedimentary strata encased within lavas of the British Tertiary Volcanic Province (BTVP), formed during rifting and formation of the North Atlantic, and represent forests that grew on the lava field during quiescent intervals. These studies have largely focussed on the taxonomy of the floras (Forbes 1851, Bailey 1869, Gardner 1887, Gardner and Ettinghausen 1879-1882, Gardner 1883-1886, Seward and Holttum 1924, Johnson 1914, 1933, 1937, Johnson and Gillmore 1921, Crane 1984, Crane 1988, Crane et al. 1988, Boulter and Kvacek 1989) and have shown that mixed conifer and angiosperm vegetation became established in solis that developed on weathered lava tops between eruptive intervals. Palynological studies of this region have also provided an understanding of vegetation patterns over wider geographical areas, as well as providing an insight into the palaeoecology of these floras (Boulter and Kvacek 1989, Jolley 1997, Jolley et al. 2009).

New collections of fossil floras from the Isle of Skye, Scotland offered an opportunity to investigate a new Paleocene flora that has not been formerly described or analysed. This flora has contributed further taxonomic information about the composition and palaeoecology of these new BTVP forests, as well as providing the first quantitative data about the palaeoclimate for this region.

1.2 Paleocene world

The Paleocene represents an interesting interval in Earth's history because significant biological and climatic events occurred during this period. Important events include the Cretaceous/Paleogene extinction (K/Pg) and biotic recovery after this event, the appearance of modern groups of organisms, volcanism in the North Atlantic, and intense global warming at the end of the Paleocene (Paleocene-Eocene Thermal Maximum, PETM)

The Paleocene spans ~10 million years from the K/Pg boundary at 65.5 ± 0.3 Ma to Paleocene/Eocene boundary at 55.8 ± 0.2 Ma (Gradstein et al. 2004). This interval is divided into three subdivisions, the Danian, Selandian and the Thanetian (Table 1.1, Figure 1.1). The Paleocene has been been divided into numerous biostratigraphic zones, shown in Figure 1.1, along with the chronostratigraphy.

Table 1.1. Paleocene ages and their duration (Ma). Age boundaries derived from Gradstein et al. (2004).

Period		Ages	Duration (Ma)
Paleocene	Late	Thanetian	58.7 ± 0.2 to 55.8 ± 0.2
		Selandian	61.7 ± 0.2 ± to 58.7 ± 0.2
	Early	Danian	65.5 ± 0.3 to 61.7 ± 0.2

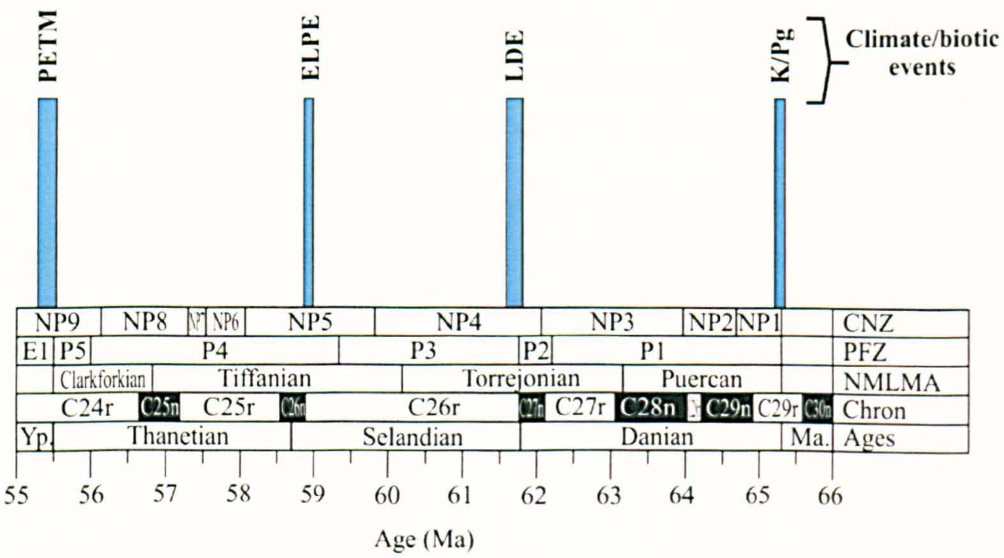

Figure 1.1. Combined magneto and biostratigraphical timescale for the Paleocene, showing major biotic and climatic events that occurred during this interval. Magnetostratigraphy (Chron) from Westerhold et al. (2008), NMLA = North American Land Mammal Ages from Alroy (2000), CNZ = Calcareous Nannoplankton Zones from Martini (1971), PFZ = Planktonic Foraminifera Zones from Breggren and Pearson (2003). Climatic and biotic events denoted by blue bars, width of blue bar denotes duration of the event. K/Pg = Cretaceous/Paleogene boundary, LDE = Late Danian Event, ELPE= Early Late Paleocene Event, PETM = Paleocene/Eocene Thermal Maximum. Figure redrawn and modified from Westerhold et al. (2011).

1.3 Paleocene climate

The Paleocene was one of the warmest intervals of the Cenozoic. Latitudinal temperature gradients were low (Corfield 1994, Zachos et al. 2001) (Figure 1.2, Figure 1.3). Globally warm climate conditions meant that the polar regions lacked ice sheets and evidence from fossil plants and sediments indicate that the climate was temperate and humid at high latitudes (e.g. Wolfe 1977, Mai 1991, McIver and Basinger 1999, Tripati 2001, Marwick 2007, Uhl et al. 2007, Herman et al. 2009). Oxygen isotope records derived from benthic foraminifera indicate that benthic marine temperatures during the Paleocene were warm and ranged from ~6°C to 12°C (Zachos et al. 2001, Zachos et al. 2008, Westerhold et al. 2011).

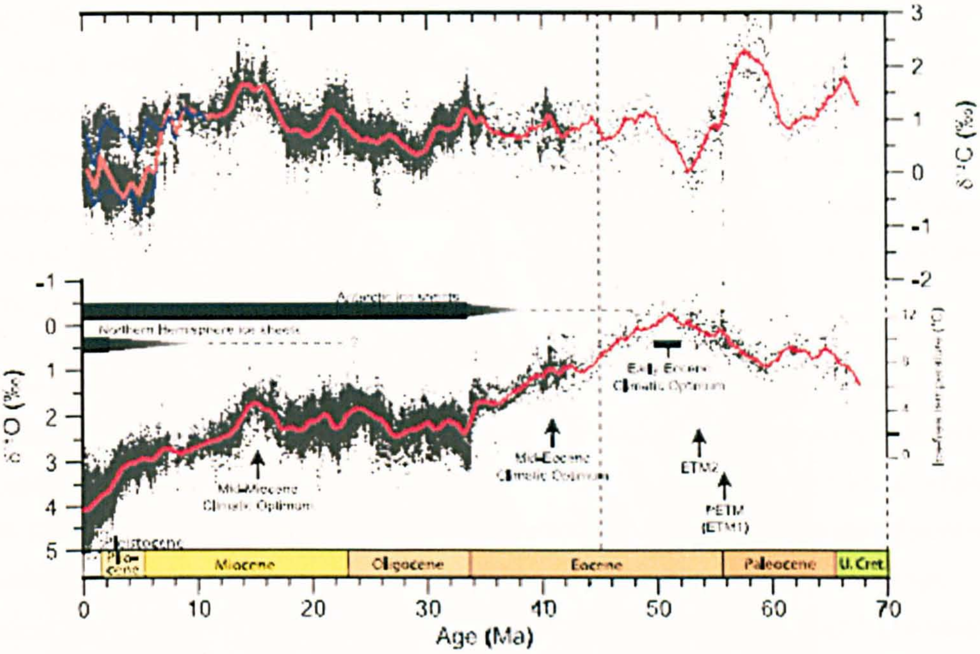

Figure 1.2. Global climate over the last 70 million years. δ13C and δ18O curved derived from benthic foraminifera from Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) sites. Red line denotes 1 million year running mean of the data. Benthic temperatures calculated from δ18O record and based on the assumption of ice free oceanic conditions. Figure taken from Zachos et al. (2008).

The distribution of sediments that are indicative of particular climate regimes have been used to reconstruct broad climatic zones for the Paleocene (Parrish et al. 1982, Scotese 2002, Markwick 2007) (Figure 1.3). The presence of coals and thermophilic organisms at the Equator indicates that the climate was tropical and humid (Parrish et al. 1982, Scotese 2002, Markwick 2007, Head et al. 2009, Wing et al. 2009). The presence of evaporite and calcrete deposits adjacent to the tropics indicates that the climates of the low to mid latitudes were arid or seasonally arid (Parrish et al. 1982, Scotese 2002, Markwick 2007). Bauxites, laterites, coals and kaolinite deposits in mid latitudes indicate that the climate was warm-temperate and humid (Parrish et al. 1982, Scotese 2002, Markwick 2007). Polar climates appear to have been cool temperate for much of the Paleocene as sediments indicative of warmer climates such as bauxites, laterites and evaporates are absent (Parrish et al. 1982, Scotese 2002, Markwick 2007).

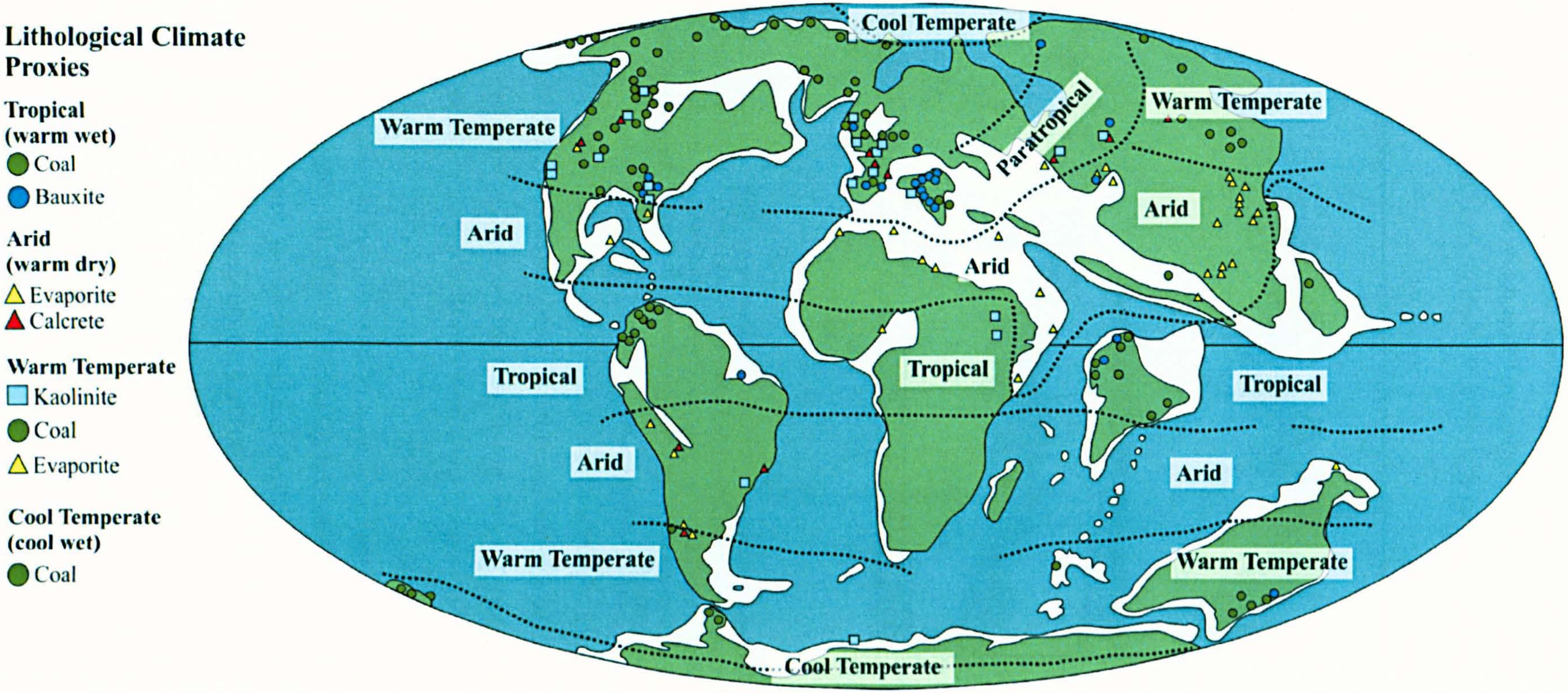

Figure 1.3. Paleogeographic map of the Late Paleocene, showing the distribution of lithological climate proxies and climatic boundaries. Redrawn from Scotese 2002.

Fossil floras have provided quantitative palaeoclimate estimates for the terrestrial realm of the Paleocene. Mean annual temperate estimates derived from mid latitude North American floras, and range from near tropical 23.2 ± 2°C to temperate 6.5 ± 2.5 °C (Wolfe et al. 1986, Davies-Vollum 1997). This is in contrast to the lithological evidence, which suggests that the climate of much of North America was warm temperate (Figure 1.3). The climatic variability in the mid latitudes of North America has been related to several factors, such as climate change after the K/Pg event, climatic variation in the Paleocene (i.e. warming and cooling), latitudinal variation, and local variations in topography and climate (Hickey 1980, Wolfe et al. 1986, Davies-Vollum 1997, Johnson and Ellis 2002, Peppe 2010). Floras from the Western Interior of the United States (Wyoming, Montana, North Dakota, South Dakota and Colorado) indicate that the climate in this region was primarily temperate to warm-temperate throughout much of the Paleocene with MAT ranging from ~5°C to 13°C (Hickey 1980, Wing 1998, Wilf 2000, Peppe 2010).

Oxygen isotopes from benthic foraminifera have provided a record of benthic marine temperatures throughout the Paleocene. This record indicates that benthic marine temperatures changed significantly through the course of the Paleocene (Kennett and Stott 1991, Corfield 1994, Zachos et al. 2001, Zachos et al. 2008, Westerhold et al. 2011). Temperatures increased in the early Danian as the climate warmed in the Early Paleocene. This warming trend was followed by a period of cooling in the oceans from the late Danian until the early Thanetian. This cooling was followed by warming throughout the Thanetian, which terminated in a transient (< 20 000 year) global warming event at the end of the Paleocene, the PETM (Kennett and Stott 1991, Zachos et al. 1993).

Considerable research has been undertaken on the PETM to determine its initiation, duration and intensity (e.g. Kennett and Stott 1991, Zachos et al. 1993, Zachos et al. 2003, Zachos et al. 2005, Higgins and Schrag 2006, Zachos et al. 2006, Roehl et al. 2007). The PETM began at 55.8 Ma and is marked by a negative peak of carbon and oxygen isotopes (Kennet and Stott 1991, Zachos et al. 1993). Evidence from benthic and planktonic foraminifera indicate that global temperatures may have increased by ~6 °C to 8°C in less than 20 000 years (Kennett and Stott 1991, Thomas and Shackleton 1996, Katz et al. 1999).

The causal mechanisms for the PETM have been highly debated and have been linked to multiple mechanisms, which include bolide impact, volcanism, changes in ocean circulation, biomass burning and methane hydrates (e.g. Katz, et al. 1999, Svensen et al. 2004, Cramer and Kent 2005, Tripati and Elderfield 2005).

Although the exact causal mechanisms for the PETM have not been determined its effects on the biosphere have been well documented. The PETM caused a major extinction of benthic foraminifera as temperatures in deeper waters increased dramatically (Kennett and Stott 1991). Planktonic foraminifera diversified and the dinoflagellate *Apectodinium* dominated marine sequences in response to the PETM (Bujak and Brinkhuis 1998, Heilmann-Clausen and Egger 2000, Crouch et al., 2001, Scheibner et al. 2005).

Terrestrial vegetation was also greatly affected. Floral records from North America show that subtropical and paratropical vegetation migrated northward in response to warming (Harrington et al. 2001, Harrington et al. 2005). Leaf damage caused by insect herbivory prior to the PETM was of low diversity and intensity, but during the warming event both diversity and intensity increased substantially (Currano et al. 2008). Mammalian diversity also changed in response to the PETM, resulting in the greatest mammalian diversity of the Paleocene (Clyde and Gingerich 1998).

Other warming events have been recognised in the Paleocene and include the Late Danian Event (LDE) and the late Early Paleocene Event (LEPE) (Westerhold et al. 2011) (Figure 1.1). These warming events were of lower intensity compared to the PETM but demonstrate that rapid warming episodes were a significant feature of the Paleocene climatic regime (Westerhold et al. 2011).

1.4 Paleocene floras of the Northern hemisphere

Paleocene fossil floras have provided an important insight into vegetation patterns at the beginning of the early Cenozoic, and have provided a wealth of information on plant systematics and evolution, on palaeoecology, as well as information on the response of vegetation to climate change. The Paleocene record of vegetation indicates that plants were diversifying rapidly and many modern groups appeared during this interval (Manchester 1999, Collinson and Hooker 2003).

Paleocene floras have been described from across the Northern Hemisphere and include sites in the North America, Asia, Europe and the Arctic, and have provided an insight into the vegetation cover during the Paleocene and how it varied longitudinally and latitudinally.

Vegetation in the high northern latitudes has been termed the Arcto-Tertiary floral zone. This floral zone is characterised by a variety of broadleaved deciduous angiosperms, conifers, herbaceous angiosperms and ferns (Mai 1991, Collinson 2001, Kvacek 2010). The use of term Arcto-Tertiary floral zone has been questioned, however, and vegetation of the Arctic has been referred to as polar deciduous forest or mixed-mesophytic forest, based on its composition and character (Wolfe 1977, Collinson and Hooker 2003). In this study the term Arcto-Tertiary is applied as it represents a useful term to describe this type of vegetation. It is used here to refer to vegetation with predominately deciduous character composed of broadleaved angiosperms and conifers.

Common broadleaved angiosperm families characteristic of this floral zone include members of the Platanaceae (planes), Cercidiphyllaceae (katsura), Betulaceae (hazel), Fagaceae (birch), Juglandaceae (walnut), Ulmaceae (elm), Vitaceae (grape vine), Cornaceae (dogwood), Trochodendraceae (trochodendron) and the Hamamelidaceae (witch hazel). Important conifer families include the Cupressaceae (redwood), Pinaceae (pine) and Taxaceae (yew). In particular, deciduous conifers such as *Metasequoia* (dawn redwood) and *Glyptostrobus* (swamp cypress) are ecologically dominant components of this floral zone (Chaney 1950, Koch 1963, Wolfe 1977, Mai 1991, Mai 1995, Kvacek et al. 1994, McIver and Basinger 1999, Collinson 2002, Collinson and Hooker 2003, LePage 2007). Figure 1.4 depicts a typical Arcto-Tertiary swamp community.

Arcto-Tertiary floras are associated with cool-temperate to warm temperate climates with high humidity, and those growing in the Arctic Circle would have been subject to seasonal light variation (Koch 1963, Mai 1991, Mai 1995, McIver and Basinger 1999, Uhl et al. 2007, Kvacek 2010). The Arcto-Tertiary floral zone persisted from the Late Cretaceous into late Paleogene, where cooling climates restricted its distribution.

Paleocene vegetation in the mid latitudes of the Northern Hemisphere contained a mix of some Arcto-Tertiary elements and other components with a more thermophilic character. The combination of temperate taxa with subtropical to paratropical elements is of note, as no modern analogues exist where these elements coexist (Collinson and Hooker 2003). Fossil plants of this type have been reported from Europe, Asia and North America, which suggests this type of vegetation was widespread during the Paleocene. These subtropical and paratropical forests are typically dominated by angiosperms with rare occurrences of conifer and ferns (Mai 1995, Manchester 1999, Collinson and Hooker 2003, Kvacek 2010, Pigg and DeVore 2010). The composition of this mixed forest type varied regionally but was distinguished from the more temperate vegetation further north primarily by its physiognomy. The broadleaved angiosperm components of these floras had characteristic leaf physiognomies with entire margins, thick coriaceous textures that indicate that they were evergreen (Mai 1995, Collinson and Hooker 2003 Kvacek 2010).

Figure 1.4. Reconstruction of a Paleocene Arcto-Teriary flora. Depicted is a swamp community dominated by the deciduous conifer *Metasequoia*, with an understory composed of woody angiosperms such as *Corylites* (Betulaceae) and *Trochodendroides* (Cercidiphyllaceae), the fern *Onoclea* and *Equisetum* (horsetail). Reconstruction by Jon Poulter.

Characteristic elements of this vegetation type included members of the families Arecaceae (palms), Fagaceae (oak), Lauraceae (laurels) and Zingiberaceae (ginger), and forms whose affinities cannot be determined but have characteristic morphologies, such as entire margins and thick coriaceous leaf textures indicative of warmer climates (Mai 1995, Manchester 1999, Collinson and Hooker 2003, Kvacek 2010, Pigg and DeVore 2010). Tropical rainforests have also been documented in the mid latitudes in the Paleocene. The Castle Rock flora from Colorado in the United States represents a diverse floral community that was growing in a warm humid climate indicative of tropical rainforest conditions (Johnson and Ellis 2002) (Figure 1.5). One of the most remarkable aspects of this flora is its age. The Castle Rock flora has been dated as 64.1 Ma, which suggests that diverse floral communities had developed relatively rapidly after the K/Pg mass extinction in North America.

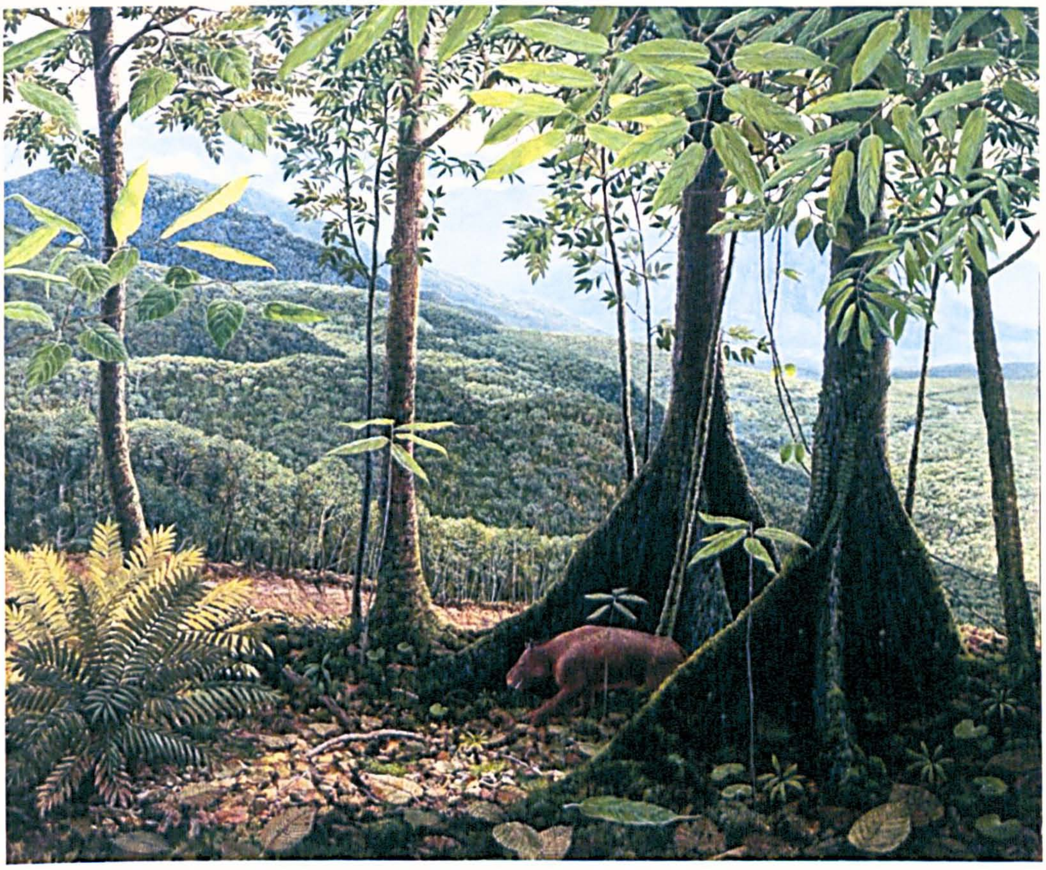

Figure 1.5. Artistic reconstruction of a 64 million year old tropical rainforest from Castle Rock Colorado, United states. Scene depicts rainforest growing along the flanks of the Rocky Mountains. Vegetation dominated by woody angiosperm trees that possess large, entire margined leaves with drip-tips. Understorey vegetation composed of herbaceous angiosperms and cycads. The mammal Stylinodontine taeniodont is depicted in the foreground. Artist Jan Variesen, image taken from Denver Museum of Natural History website (www.dmns.org).

1.5 North Atlantic Igneous Province Volcanism

The North Atlantic Igneous Province (NAIP) is one of the largest Continental Flood Basalt (CFB) provinces of the Phanerozoic (Coffin and Eldholm 1994, Eldholm and Grue 1994). The NAIP covered a wide area and includes large areas of the east and west Greenland-Baffin Corridor, the Faeroe Isles, western Scotland and Northern Ireland (Figure 1.6). Estimations of the scale of the NAIP propose that, if the volcanic margins are included, the total area was 1.3 $x10^6$ km^2 with an estimated volume of 1.8 x 10^6 km^3 (Eldholm and Grue 1994, Saunders et al. 1997). Eruption rates were equally high with an estimate of 0.6 km^3/yr (Eldholm and Grue 1994). Eldholm and Grue (1994) produced a second eruption rate estimate, assuming that if two thirds of the basalts were emplaced within 0.5 m.y., then eruption rates would have been 2.4 km^3/yr.

The NAIP underwent two phases of activity, the first (pre-breakup phase) began approximately 62 - 61 Ma in west and southwest Greenland and in northwest Britain and continued until ~59 Ma (Saunders et al. 1997, Storey et al. 1998, Courtillot and Renne 2003, Chambers et al. 2004, Storey 2007) (Table 1.2). This phase of volcanism did not lead to the formation of the North Atlantic Ocean, but led to the generation of major plateau lava sequences in west Greenland, Northern Ireland and Scotland (Saunders et al. 1997, Storey et al. 1998, Courtillot and Renne 2003, Chambers et al. 2005, Storey 2007).

The second phase of NAIP volcanism (syn-breakup phase) began at ~56 Ma and continued to ~54 Ma with eruptions centred in east Greenland and the Rockhall Plateau (Saunders et al. 1997, Storey et al. 1998, Courtillot and Renne 2003, Chambers et al. 2004, Storey 2007) (Table 1.2). This phase of volcanism was more voluminous than the first phase and led to the break-up of North Atlantic and the eventual separation of Greenland from northern Britain and Europe in the Late Paleocene at ~55 Ma (Saunders et al. 1997, Storey et al. 1998, Courtillot and Renne 2003, Chambers et al. 2005, Storey 2007).

The cause of the volcanic activity in the North Atlantic is related to the rifting and breakup of the Greenland and European landmasses and the formation of the North Atlantic Ridge (Saunders et al. 1997). The development of the Icelandic mantle plume in the North Atlantic has been postulated as major causal mechanism for the development of this CFB (Storey et al. 2007). Other mechanisms have been suggested to have led to the development of the NAIP and include crustal delamination, bolide impact, small-scale rift-related convection, and chemical mantle heterogeneities (Meyer et al. 2007). Meyer et al. (2007) reviewed these possible mechanisms and found that delamination and bolide impact did not support the current evidence of the NAIP formation, but small-scale rift-related convection may have contributed to the formation of the NAIP.

The British Tertiary Volcanic Province (BTVP) represents a sub-province within the NAIP. The BTVP is composed of extensive lava sequences in Northern Ireland and the Hebrides. Included in this province are a range of intrusive bodies that range from dykes and sills to plutons, which represent the edifices of central volcanoes. The BTVP formed within first phase of NAIP volcanism, with magmatic activity beginning ~62 to 61 Ma and continued until ~59 Ma (Chambers et al. 2005, Ganerød et al. 2010). The BTVP is of interest to this study as interbasaltic sediments between the lavas flows contain fossil plant remains that have been used in this investigation. A more extensive review of the BTVP is presented in Chapter 2.

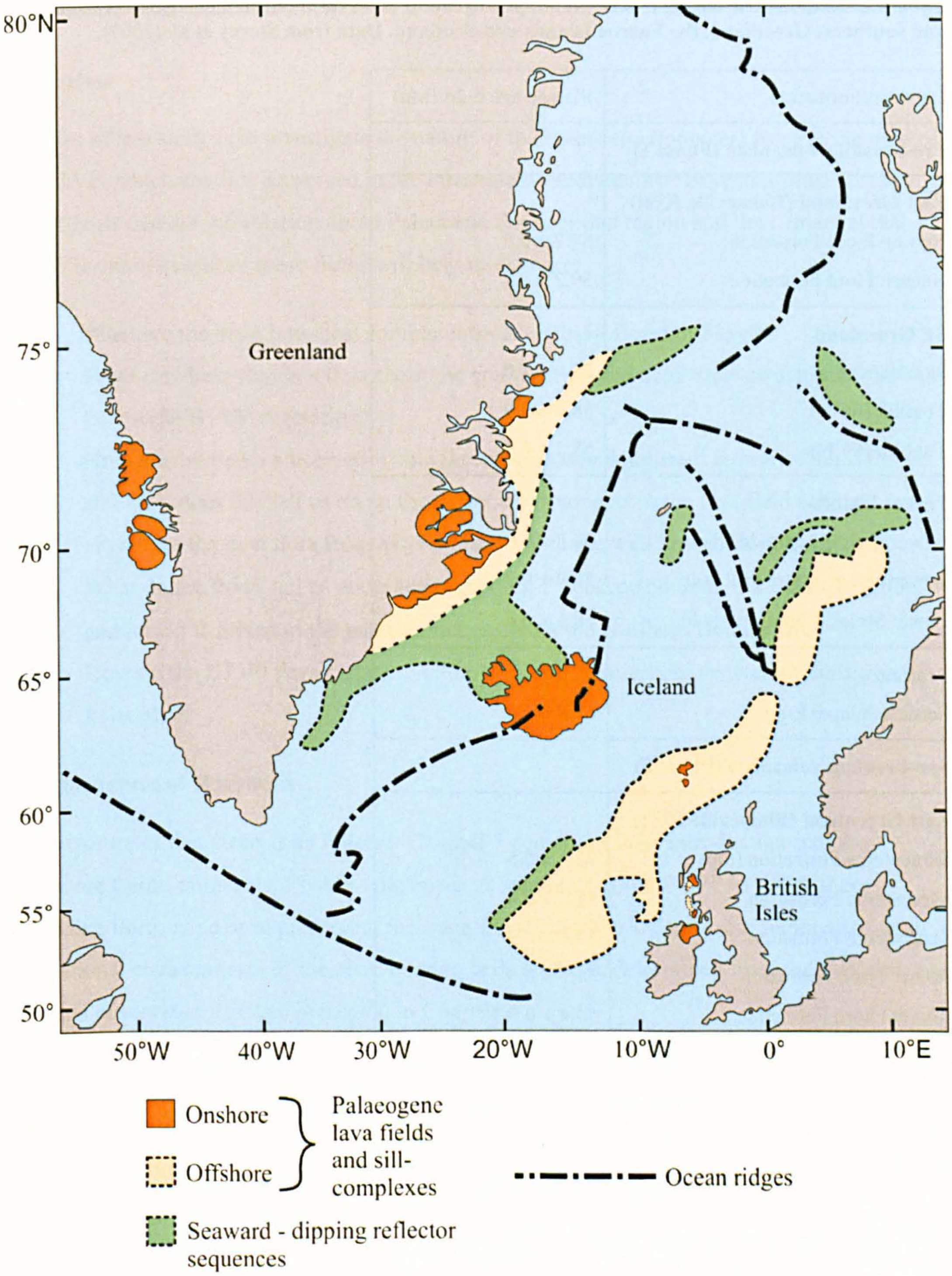

Figure 1.6. The North Atlantic Igneous Province (NAIP) showing the onshore and offshore igneous sequences and seaward-dipping reflector sequences. Redrawn from Saunders et al. (1997).

Table 1.2. Radiometric dating ($^{40}Ar/^{39}Ar$) of pre-breakup and syn-breakup igneous rocks from east and southeast Greenland, the Faeroe Islands and Scotland. Data from Storey et al. (2007).

Location/Formation	Plateau age ± 2σ (Ma)
Pre-breakup volcanism (Phase 1)	
East Greenland (Blosseville Kyst)	
Nansen Fjord Formation	57.7 ± 0.5
Nansen Fjord Formation	59.2 ± 1.4
SE Greenland	
Skjoldungen	61.4 ± 1.0
Tugtilik (66°N)	58.3 ± 0.9
Tugtilik (66°N)	58.3 ± 0.9
Faeroe Islands	
Lower Series, Lopra drill hole	56.8 ± 0.6
Lower Series, Lopra drill hole	59.9 ± 0.7
Lower Series, Lopra drill hole	60.1 ± 0.6
Scotland	
Felsic ash layer Eigg	61.8 ± 1.0
Syn-breakup volcanism (Phase 2)	
East Greenland (Blosseville Kyst)	
Skraenterne Formation (top)	55.1 ± 0.5
Skraenterne Formation	55.0 ± 0.4
Skraenterne Formation	54.9 ± 0.9
Romer Fjord Formation	55.1 ± 0.5
Romer Fkord Formation	54.4 ± 0.9
MilneLand Formation	56.1 ± 0.5
Faeroe Islands	
Upper Series	55.2 ± 0.7
Middle Series	54.9 ± 0.7

1.6 Thesis aims and structure

1.6.1 Aims

The aim of this study is to investigate the nature of the Paleocene floras that lived at the time of the BTVP, which are now preserved in the interbasaltic sediments of Skye and Mull. These plant fossils contain information about Paleocene floras of this region and the climate at that time. The main questions these floras will help answer are:

1. What are the main botanical components of the fossil floras of Skye?
2. What can these fossils tell us about the composition and ecosystem structure of the Paleocene BTVP vegetation?
3. How are the floras preserved within the volcanically dominated terrain of the BTVP, and what does this tell us about the palaeoenvironments in the lava field setting?
4. How does the new flora from Skye compare with the well known flora from Mull?
5. What do the floras tell us about the prevailing Paleocene climate of the BTVP region and how it is linked to the palaeoclimates across the Northern Hemisphere?
6. How do the BTVP floras relate to other Northern Hemisphere vegetation during the Paleocene?

1.6.2 Structure of this thesis

The structure of this thesis is as follows: Chapter 1 contains a brief introduction into the Paleocene floras, climate and NAIP volcanism. A summary of the BTVP in which these Paleocene floras have been preserved, their age from radiometric dating, the sedimentary and depositional environments of the plant bearing beds on Skye, determined from the literature and personal observations is then presented in Chapter 2.

Chapter 3 includes a discussion about the preservation of the angiosperm leaves and descriptions of the angiosperm leaf morphotypes from Skye. Conifers are described in Chapter 4. The reconstruction of the vegetation of the Skye fossil leaf assemblages is presented in Chapter 5, with additional information from the published palynological record.

Palaeoclimate analysis of the angiosperm leaf morphotypes of Skye, using Leaf Margin Analysis (LMA), Climate Leaf Analysis Multivariate Program (CLAMP) and Multiple Linear Regression Models (MLR), is presented in Chapter 6. The Palaeoclimate data from the plants are compared to that from other climate proxies.

The Paleocene vegetation of Mull is discussed in Chapter 7, based on published records and new observations, this is compared with results from this study on the Skye flora. Palaeoclimate data from the Mull flora from this project are presented and compared to palaeoclimate data derived from the Skye flora.

Chapter 8 brings together the results and compares the BTVP flora with those of other Northern Hemisphere regions, discusses how the BTVP volcanism may have affected BTVP vegetation, and how the climate record derived from the BTVP plants relates to the global Paleocene record. The main conclusions from this study are presented in Chapter 9.

Chapter 2: Geological setting

2.1 Introduction

Presented here is the geological of the British Tertiary Volcanic Province (BTVP), which is discussed in order to understand the environments in which the floras of this province lived. Understanding the chronological development of the BTVP is vital to provide a detailed temporal framework of the province as a whole, and provide precise ages of the fossil floras. The geological setting of the volcanic province is discussed in the context of the mechanisms involved in its formation, which provides a broader regional setting. The chronological phases of the BTVP development are described and the relative timing and duration of the constituent parts are outlined, with special reference to the lava fields. The sedimentary sequences of the BTVP are also outlined. Specific detail is given on the plant-bearing formations of Skye, with information regarding the depositional environments that gave rise to their formation. Determining the sedimentary environments in which the fossil floras grew is vital to understand how they were deposited and what palaeoenvironments they inhabited.

2.2 Geological setting of the British Tertiary Volcanic Province (BTVP)

The Paleocene igneous rocks of the Hebrides and Northern Ireland represent a sub-province within the North Atlantic Igneous Province (see Chapter 1 section 1.5). This sub-province is called the British Tertiary Volcanic Province (BTVP), which consists of extensive, predominately basaltic sub-aerial lava fields, dyke swarms and igneous intrusions ranging from sill complexes to the larger central complexes, which represent the roots of central volcanoes (Figures 2.1, 2.2) (Emeleus and Bell 2005).

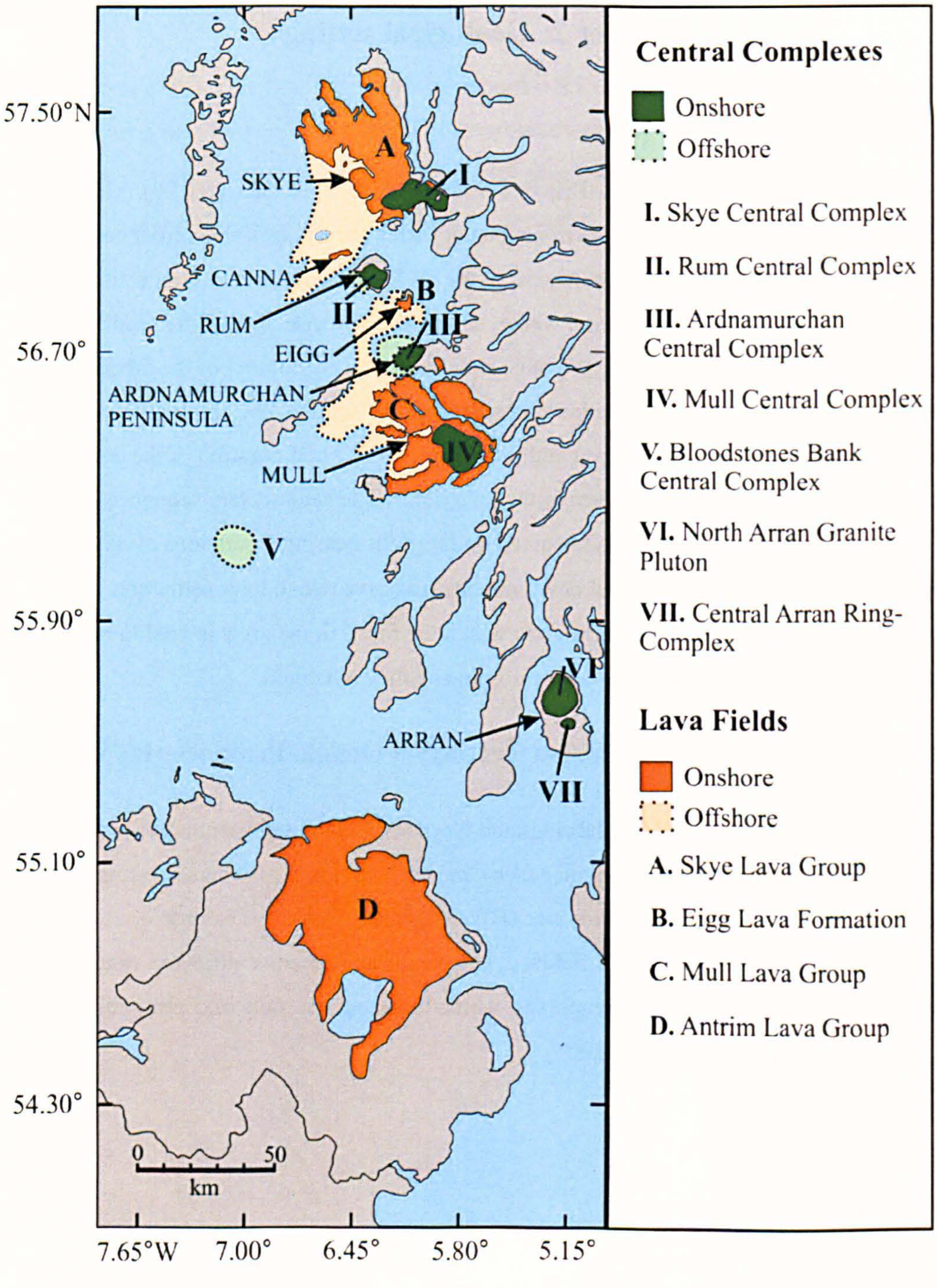

Figure 2.1. The British Tertiary Volcanic Province (BTVP) showing the extent of the offshore lava fields and the central complexes. Redrawn and modified from Emeleus and Bell (2005).

The presence of sedimentary and volcanoclastic sequences, and fossil plant assemblages preserved within the lava fields indicate that volcanic activity was not continuous (Boulter and Kvacek 1989, Williamson and Bell 1994, Jolley 1997) (Figure 2.2). The sedimentary sequences indicate that a variety of sedimentary processes and depositional environments developed on the lava fields during volcanic quiescent intervals.

Mass-movement and debris flow deposits occur across the BTVP, with notable deposits present in the Preshal Beg Conglomerate Formation, west-central Skye, Malcolm's Point, Mull and Achateny, Ardnamurchan (Brown et al. 2009). These deposits indicate that catastrophic deposition was common place, particularly during the early phases of quiescent intervals (Williamson and Bell, 1994, Brown et al., 2009).

Fluvial and lacustrine deposits indicative of braided rivers and overbank deposition are less frequently preserved but are locally extensive, such as those of the Minginish Conglomerate Formation of west-central Skye (Williamson and Bell 1994, Brown et al., 2009). Associated with these facies are coals and plant rich siltstones (Williamson and Bell 1994, Brown et al. 2009), indicating that these environments were vegetated. These include the floras of Ardtun on Mull and Allt Mor on Skye, which are studied here.

The presence of laterites and other weathering related deposits occur throughout the BTVP (Williamson and Bell 1994, Kerr 1995, Hill et al. 2000, Brown et al. 2009); this indicates that the local climate had a strong influence on the volcanic landscape. Figure 2.3 shows a generalised schematic diagram of the sedimentary processes and environments that were present in the BTVP during the Paleocene.

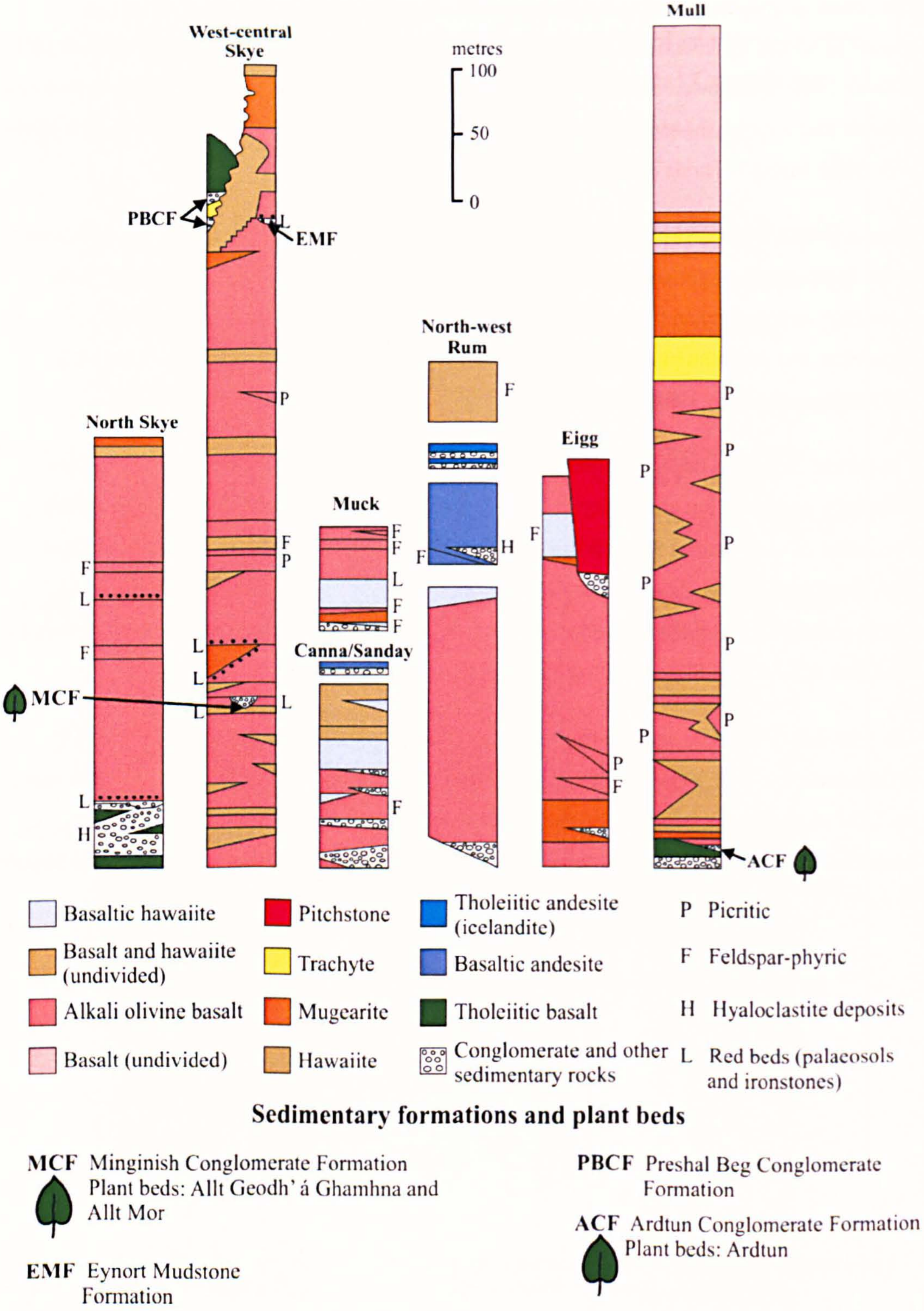

Figure 2.2. Generalised and composite vertical sections of the lava fields of the BTVP. Location of major sedimentary formations and plant beds within the lava fields given. (Redrawn and modified from Emeleus and Bell, (2005).

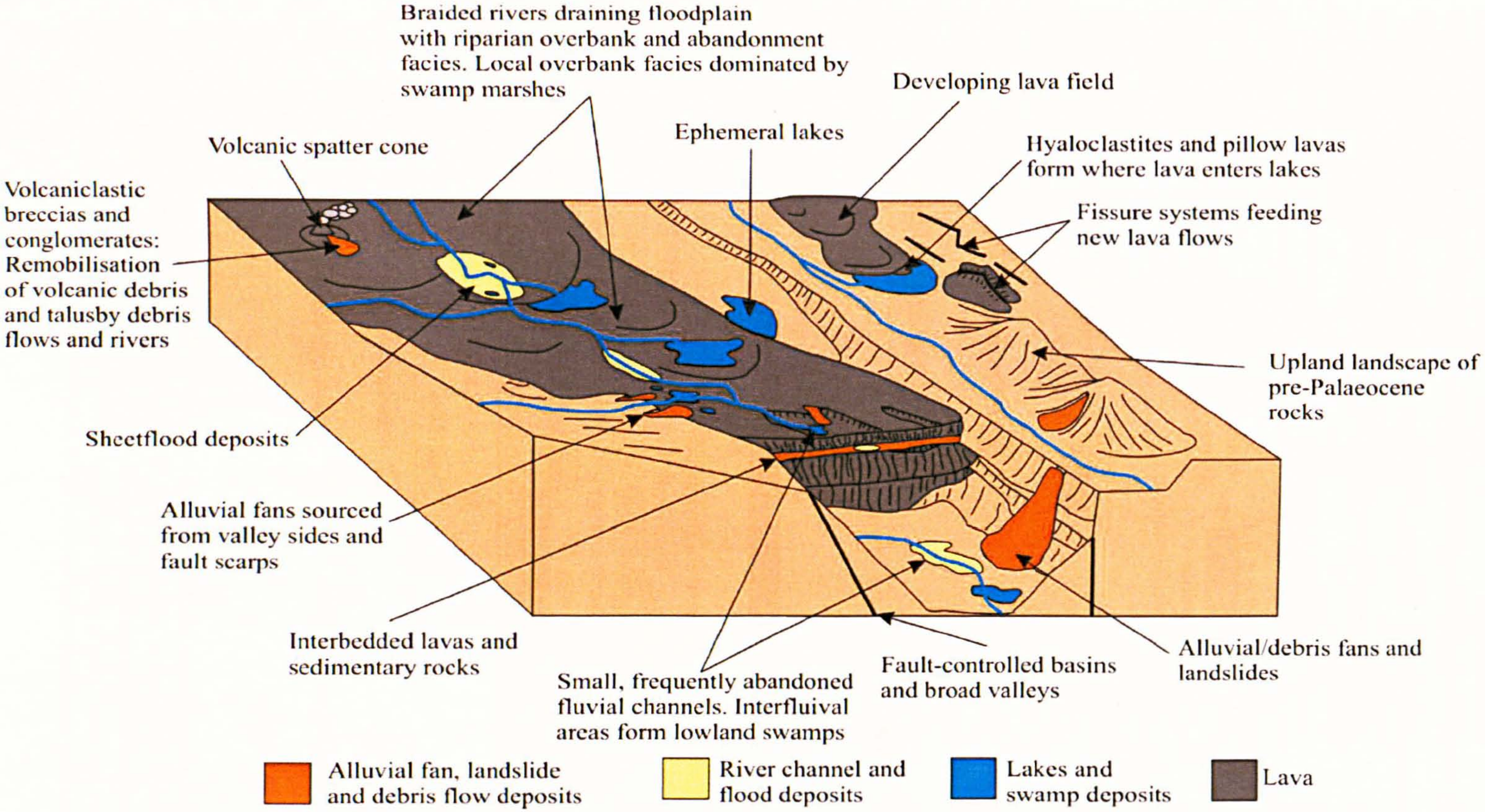

Figure 2.3. Generalised schematic diagram of the sedimentary processes and environments that developed on the pre and post volcanic landscape of the BTVP. Redrawn and modified from Brown et al. (2009).

2.3 Evolution and chronological development of the BTVP

The temporal evolution of the BTVP has been established in numerous studies through stratigraphic relationships and radiometric dating of various igneous rocks. The radiometric dating and cross-cutting relationships preserved within the BTVP indicate igneous activity initiated across the province at ~62-61 Ma (Emeleus and Bell 2005). The major lava fields developed rapidly between ~61-58 Ma (Figure 2.4). This phase of volcanism was followed by the establishment of the central complexes, which were active during and after the formation of the lava fields (Emeleus and Bell 2005). Figure 2.4 summarises the current radiometric dating of the BTVP and Tables 2.1 and 2.2 display the ages of the lava fields and central complexes.

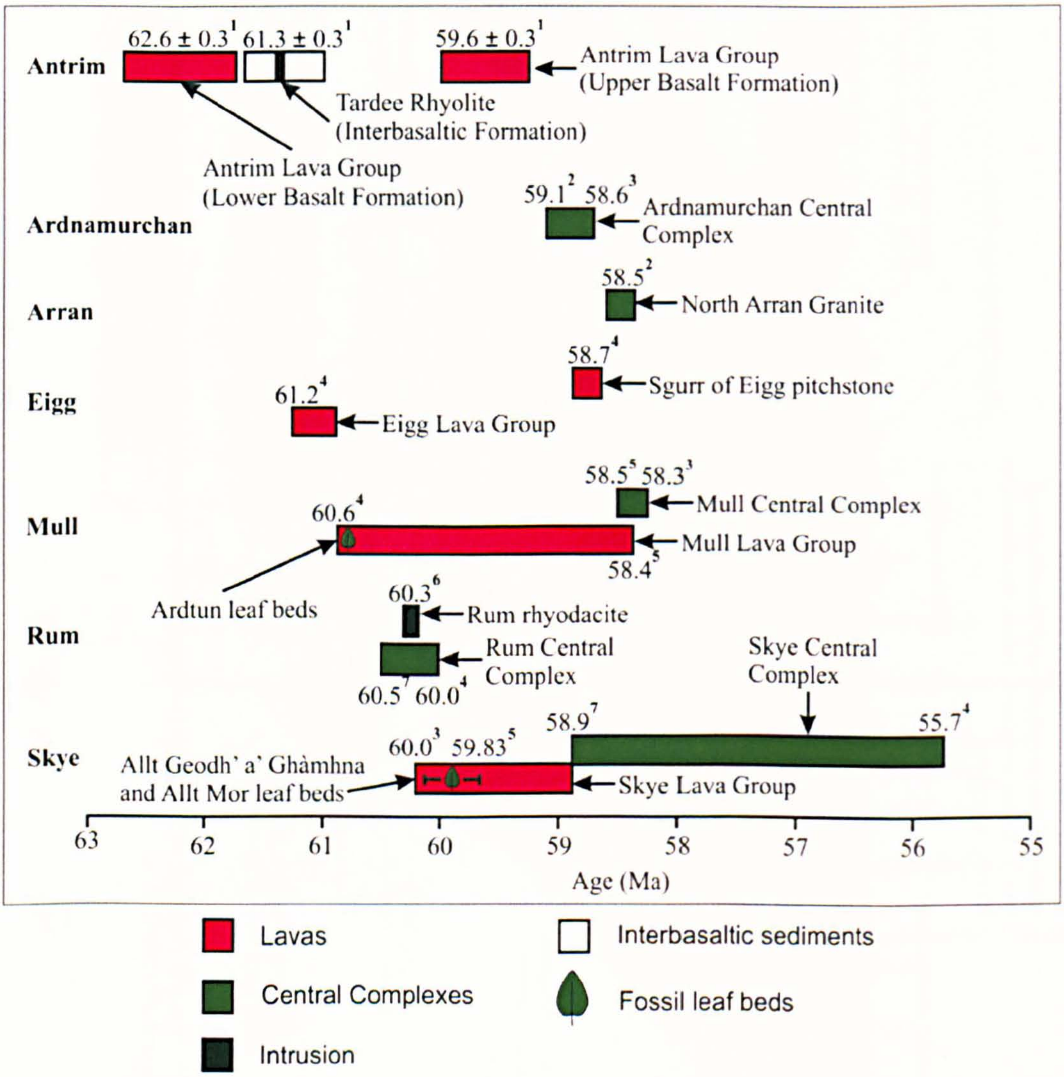

Figure 2.4. Chronological development of the magmatic activity of the BTVP based on field relationships and radiometric dating. 1. Ganerød et al. (2010) (Ar/Ar); 2. Chambers (2000) (Ar/Ar); 3. M.A. Hamilton unpublished data reported in Emeleus and Bell (2005) (U/Pb); 4. Chambers et al. (2005) (Ar/Ar); 5. Chambers and Pringle (2001) (Ar/Ar); 6 Troll et al. (2008) (Ar/Ar); 7. Hamilton et al. (1998) (U/Pb). Modified, updated and redrawn from Brown et al. (2009).

Table 2.1. Age Determinations for the lava sequences of the BTVP. Ages are million years (Ma). Collated and updated from Emeleus and bell (2005).

Locality	Age	Method	Source
Antrim Lava Group			
Lower Basaltic Formation	62.6 ± 0.3	Ar-Ar	1
Tardee Rhyolite, Interbasaltic Formation	61.3 62.6 ± 0.3	Ar-Ar	1
Upper Basaltic Formation	59.6 62.6 ± 0.3	Ar-Ar	1
Eigg Lava Formation			
Sanidine in tuff near base of formation on Muck	60.56 ± 0.07	Ar-Ar	2, 3
Zircon in same tuff	61.15 ± 0.25	U-Pb	3
Mull Lava Group			
Staffa Lava Formation	55-54.5	Palynology	4
(Includes the fossil plant deposits of Ardtun)	60.56 ± 0.29	Ar-Ar	5
	58.35 ± 0.19	Ar-Ar	5
Mull Plateau Lava Formation (top)	60.57 ± 0.24	Ar-Ar	#
Trachytic tuff, Calgary Bay	60.5 ± 0.3	Ar-Ar	*
Canna Lava Formation			
Hawaiites	60.00 ± 0.23	Ar-Ar	3
Conglomerates within lavas, Rum and Canna	58.0-58.25	Palynology	4
Skye Lava Group			
Sedimentary rocks of the Skye Lava Group	58-58.25	Palynology	4
(Includes the fossil plant deposits of Allt Geodh' a' Ghamhna and Allt Mor)			
Sledale Trachytic Tuff, Skye Lava Group, Below Preshal Beg Conglomerate Formation	58.91 ± 0.1	Ar-Ar	8

All radiometric age determinations quoted at the 2 sigma level, except source 1 and 5 which are at the 1 sigma level. 1. Ganerød et al. (2010), 2. Pearson et al. (1996), 3. Chambers et al. (2005), 4. Jolley (1997), 5. Chambers and Pringle (2001), 6. Bell and Williamson (2002). # unpublished Ar-Ar analysis by S.P. Kelley (Open University). Reported in Emeleus and Bell (2005). *Unpublished U-Pb analysis by M.A. Hamilton, Jack Satterly Geochonogy Laboratory, Department of Geology, University of Toronto.

Table 2.2. Age determinations for central complexes of the BTVP. Ages are million years (Ma). Collated from Emeleus and Bell (2005).

Locality	Age	Method	Source	
Ardnamurchan Central Complex				
Great Eucrite, pegmatic gabbro, Centre 3	59.05	Ar-Ar	1	5
Tonalite, Centre 3	58.6 ± 0.2	U-Pb	*	*
Mull Central Complex				
Loch Ba Felsite, Centre 3	58 ± 0.1	U-Pb	*	*
	58.48 ± 0.18	Ar-Ar	2	6
Corra Bheinn Gabbro, Centre 2	58.3	U-Pb	*	*
Skye Central Complex				
Eastern Red Hills Centre				
Beinn an Dubhaich Granite	55.89 ± 0.15	U-Pb	*	*
Pitchstone dyke cutting Beinn na Callich Granite	55.7 ± 0.1	U-Pb	*	*
Western Red Hills Centre				
Marsco Granite	58.4 ± 2.1	U-Pb	*	*
Southern Porphyritic Granite	57 ± 0.5	U-Pb	*	*
Loch Ainort granite	58.58 ± 0.13	Ar-Ar	2	6
Srath na Creitheach Centre				
Ruadh Stac Granite	57.5	Ar-Ar	1	5
Cullin Centre				
Coire Uaigneich Granite	59.3 ± 0.7	Rb-Sr	3	4
Pegmatic facies of Outer Gabbro	58.91 ± 0.08	U-Pb	4	2
Arran				
North Arran Granite Pluton	58, 58.4	Ar-Ar	1	5

All radiometric age determinations quoted at the 2 sigma level, except references 1 and 2 which are at the 1 sigma level. 1. Chambers (2000), 2. Chambers and Pringle (2001), 3. Dickin (1981), 4. Hamilton et al. (1998). *Unpublished U-Pb analysis by M.A. Hamilton, Jack Satterly Geochonogy Laboratory, Department of Geology, University of Toronto.

2.3.1 Lava fields

The Lava fields of the BTVP were an important influence on the floras that grew in this region during the Paleocene. The lava fields and surrounding pre-Paleocene rocks provided the substrate on which the floras colonised and developed. Determining the structure and chronological development of the lava fields enables a more detailed understanding of the age of the floras, and how they may have developed in this landscape. The structure, size and chronological development of the Skye Lava Group is of direct relevance for this study as these lavas contain the fossil leaf beds (Figure 2.4).

2.3.1.1 Skye Lava Group (SLG): West-central Skye

The Skye Lava Group (SLG) is subdivided into multiple sub-groups and volcanic sedimentary sequences in west-central and northern Skye and Canna (Williamson and Bell, 1994, Bell and Williamson 2002). The SLG unconformably overlies Mesozoic and Neoproterozoic sediments (Williamson and Bell 1994, Bell and Williamson 2002). Eight main lava sub-groups comprise the SLG in west-central Skye and include the Rubh' an Dunain, Bualintur, Cruachan, Glen Caladale, Fiskavig, Loch Dubh, Gleann Oraid and Talisker sub-groups (Williamson and Bell 1994). The SLG outcrops in west-central and northern Skye and extends to the boundary of the Skye Central Complex; the lavas of this formation extend offshore towards Canna and Rum (Figure 2.5). The current geographical extent of this lava field covers approximately 200 km^2; the thickness of these lava groups is variable and ranges from ~100-330 m, its original overall thickness is estimated as being ~1.5 km (England 1994, Williamson and Bell 1994).

Precise dating of the SLG has been established through radiometric dating and stratigraphic relationships. The age of the lowest unit of the SLG is 60.53 ± 0.08 Ma and the upper part is 58.91± 0.07 Ma, which indicates that the lava pile formed rapidly within a maximum interval of 1.6 m.y. (Hamilton et al., 1998, Chambers and Pringle, 2001). The age of the lower unit is derived from the presence of Rum derived clasts present within the intra-basaltic sediments of the Minginish Conglomerate Formation (between the Bualintur and Cruachan lava groups). The clasts within the sedimentary sequences on Skye appear to have been derived after the formation and un-roofing of the Rum Central Volcano, which formed at 60.53 ± 0.08 Ma (Chambers et al. 2005). The upper age limit was derived from radiometric dating of the Cullin Gabbros, which cross-cut the SLG, and are therefore younger. This interval has been refined with the additional radiometric dating of the upper section of the SLG, which provided an age of 59.83 ± 0.12 Ma (Chambers and Pringle, 2001). This most recently published date indicates that the significant proportion of the SLG formed in a shorter interval of 0.9 million years.

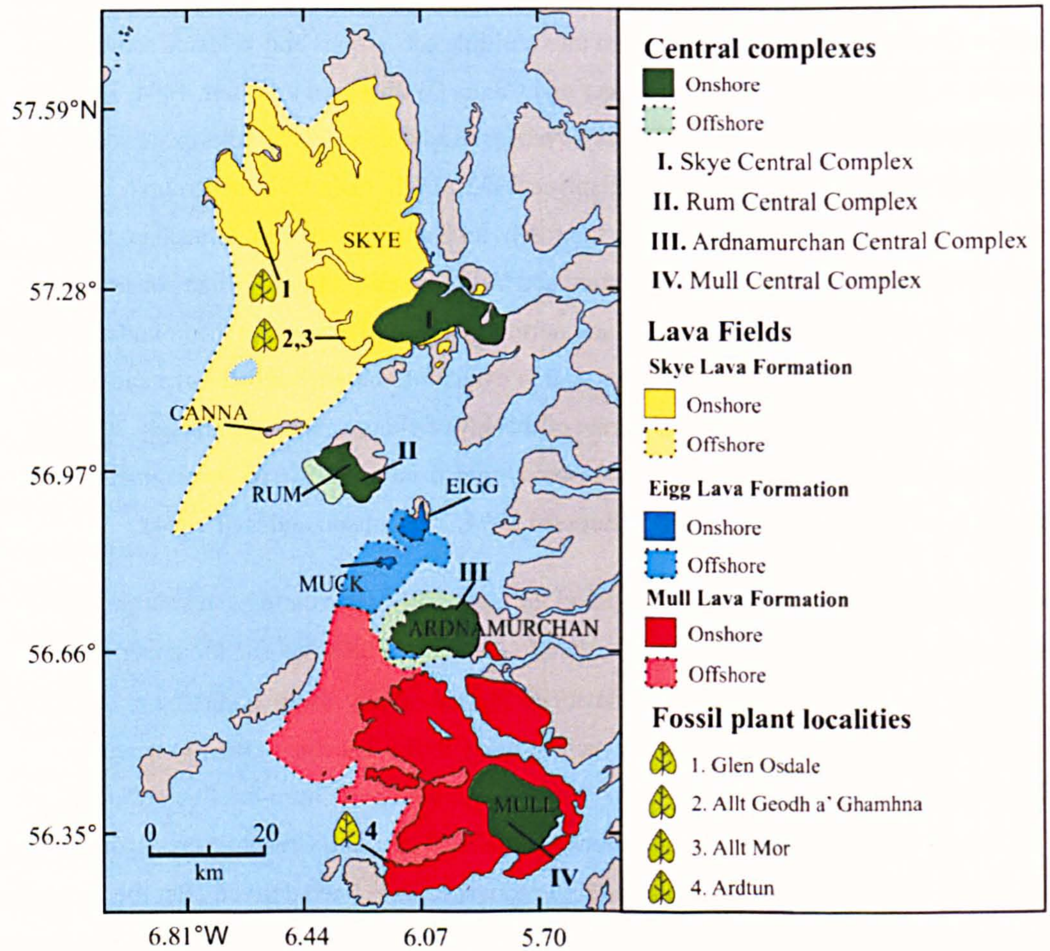

Figure 2.5. Map of lava fields, central complexes and fossil plant localities of the Inner Hebrides. Redrawn and modified from Emeleus and Bell (2005).

2.3.1.2 Skye Lava Formation: Northern Skye

The lavas of northern Skye are divided into five lava sub-groups: Beinn Edra Group, Ramascaig Group, Beinn Totaig Group, Bracadale Group and the Osdale Group (Anderson and Dunham, 1966). Radiometric dates have not been obtained from the lavas or tuff layers. Determining the stratigraphic relationships with west-central Skye is therefore difficult and it is unclear how these lava groups correlate within the development of the SLG in west-central Skye but are probably synchronous.

2.3.2 Central complexes

The volcanic rocks of the BTVP are not entirely the product of fissure-fed eruptions. A variety of central complexes occur across the breath of the BTVP (Figure 2.5). These central complexes represent eroded roots of central volcanoes. Although the central complexes vary enormously in their structure, composition and developmental history, they do have several features in common (Emeleus and Bell 2005). The majority of the central complexes are located on ridges of pre-Mesozoic rocks and in association with ancient fault systems, and the intrusions form a circular structure up to 15km across (Emeleus and Bell 2005). Central complexes are known from Skye (Cuillin, Srath na Creitheach, Western Red Hills and Eastern Red Hills centres), Rum (Rum Central Complex), Ardnamurchan (Centres 1, 2 and 3), Mull (Mull Central Complex), and Arran (North Arran Granite Pluton, Central Arran Ring-complex) (Bailey et al. 1924, Gribble et al. 1976, Bell and Harris 1986, England 1992, Emeleus 1997). Well constrained dating of many of these centres (Figure 2.4) indicates they may have formed relatively rapidly within an interval of ~1 m.y. but their development was not simultaneous.

2.3.3 Chronological summary

The dating of the lava fields and igneous centres of the BTVP indicate that the majority of the lava field development occurred between 61-59 Ma, and can be attributed to Chron26r (60.92-57.91 Ma) (Chambers et al. 2005). The relative rates of development for each component of the BTVP were variable, but often rapid. The formation of the four main lava fields occurred rapidly within maximum durations of 0.92 m.y. (Eigg Lava Formation), 3.63 m.y. (Antrim Lava Group), 2.3 m.y. (Mull Lava Formation) and 0.9 m.y. (Skye Lava Formation). The development of these substantial lava fields indicates that the rate of magma generation was high and sustained during the late Early to mid-Paleocene, and consistent with an upwelling mantle plume, similar to current volcanism in Hawai'i (Hamilton et al. 1998).

2.4 Sedimentary environments of the BTVP

Volcanic activity within the BTVP was not continuous as indicated by inter-basaltic sedimentary sequences and fossil plant remains, which occur across the province and indicate that a variety of depositional environments developed during periods of volcanic quiescence (Figure 2.4, Table 2.3).

Alluvial and fluvial deposits of braided river systems were widespread, but were best developed in the Minginish Conglomerate Formation in west-central Skye (Figure 2.2). These deposits show a cyclic pattern, beginning with conglomerate-sandstone-localised coal/siltstone deposits (Williamson and Bell 1994) (Table 2.3). These deposits represent shifts and maturation of the depositional environment from high-energy flow and channel deposits to low energy overbank and swamp pool deposits (Williamson and Bell 1994, Brown et al. 2009). Localised plant remains are present within the siltstone units (Williamson and Bell 1994, Brown et al. 2009), indicating that vegetation colonised the channel margins, flood plains and swamps associated with these braided river deposits. Similar deposits occur in the Staffa Lava Formation at Ardtun Head, Mull (Figure 2.2) and represent conglomerate-sandstone-siltstone sequences, with well preserved plant remains (Boulter and Kvacek 1989, Bell and Williamson 2002, Jolley et al. 2009).

Laterite deposits and weathered flow tops are widespread, indicating that weathering rates were high. Laterite deposits and other weathering related sequences are a common feature of many of the lava fields, and typically occur as thin horizons (Williamson and Bell 1994, Keer 1995, Bell and Williamson 2002, Brown et al. 2009). These laterite deposits can be extensive, however, for example the Interbasaltic Formation of Antrim, Northern Ireland represents lateritic deposition with localised development of up to 30 m thick (Hill et al. 2000).

Lacustrine deposits containing sediments associated with weathering products and leachates derived from the lavas occur across the BTVP, but are most well developed in parts of the SLG (Williamson and Bell 1994, Brown et al. 2009). The Eynort Mudstone Formation is preserved between the Glen Caladale and Gleann Oraid Lava Groups of west-central Skye and are typically 2-15 m thick (Figure 2.2). Sediments of this formation are composed of clays, silts, ironstones, shales, thin lignites and thick laterite deposits (Williamson and Bell 1994) (Table 2.3). These sediments are indicative of a quiescent interval characterised by intense weathering and runoff. Leachates and weathering products were then deposited in shallow, possibly ephemeral lakes and ponds that developed on the lava surface (Williamson and Bell 1994). The laterite sequences indicate that this environment underwent periods of emergence with possibly better drainage, which facilitated the development of these lateritic palaeosols.

Mass wasting deposits are a common feature of BTVP sedimentary deposits, especially during the early phases of the quiescent intervals (Brown et al. 2009). The magnitude and characteristics of the mass wasting deposits are strongly linked to the topographical setting and clast composition (Brown et al. 2009). Low level slope failures were associated with lava field settings, and major slope failures occurred at the margins of central complexes (Brown et al., 2009). Caldera collapses within the centres of some of the igneous centres have mass wasting deposits of up 500m thick and clast sizes up to 0.5km across (Brown et al. 2009).

The Preshal Beg Conglomerate Formation of west-central Skye contains sediments that are characteristic of the mass movement deposition. These deposits are up to 20 m thick and are composed of heterogenous volcaniclastic material, conglomerates, breccias, grit, sands and tuffaceous silts. These sediments have been interpreted as rapidly accumulating talus and proximal alluvial fan deposits, which are typical of mass movement deposition within the BTVP (Williamson and Bell 1994, Brown et al. 2009) (Table 2.3).

Table 2.3. Summary of principal interbasaltic sedimentary lithofacies in the lava fields of the BTVP. From Brown et al. (2009).

Interbasaltic Lithofacies	Characteristics	Examples	Interpretation
Polymict conglomerate	Massive, clast- to matrix-supported conglomerate, poorly sorted, locally with lobate geometries; clasts <1m	Skye Lava Formation: Minginish Conglomerate Formation, Preshal Beg Conglomerate Formation	Debris flow
Monomict conglomerate	Massive, clast-supported conglomerate, poorly sorted (locally breccias) clasts <1m	Skye Lava Formation: Preshal Beg Conglomerate Formation	Talus/alluvial fan deposits
Lenticular sandstone	Fine to medium, massive sandstone, laminated base	Skye Lava Formation: Minginish Conglomerate Formation	Within-channel dune deposits
Cross bedded sandstone and conglomerate	Fine to coarse, trough to planar cross bedded sandstone and well sorted, normally graded conglomerate	Skye Lava Formation: Minginish Conglomerate Formation Mull Lava Formation: Ardtun Conglomerate Formation	Channel dune/channel fill and scour (hyperconcentrated flow?)
Laminated sandstone and siltstone, claystone and coal	Fine sandstone, variable silt- to claystone, plant remains woody debris, locally carbonaceous	Skye Lava Formation: Minginish Conglomerate Formation, Eynort Mudstone Formation, Preshal Beg Conglomerate Formation Mull Lava Formation: Ardtun Conglomerate Formation	Overbank and quiescence ponds, ephemeral lakes, swamps

2.5 Chronology of the inter-basaltic sequences of Skye and Mull

As mentioned in Section 2.3, precise dating of the lava fields and igneous centres has been achieved using radiometric dating and stratigraphic relationships. The interbasaltic sequences, however, are less well constrained as relatively few have been dated specifically. Presented here are the current age estimates of the Minginish Conglomerate Formation on Skye as these contain the fossil floras of Allt Mor and Allt Geodh' a' Ghamhna used in this study.

The lavas field of the Skye Lava Group and the sedimentary sequences preserved within the flows were formed rapidly, within an interval ~0.9 m.y. between 60.53 ± 0.08 and 59.83 ± 0.12 m.y. (Hamilton et al. 1998, Chambers and Pringle 2001). Each of the major sedimentary formations, (the Minginish Conglomerate Formation, Eynort Mudstone Formation and the Preshal Beg Conglomerate Formation) represent quiescent intervals, during which extrusive activity had either ceased or lessened dramatically. Since radiometric dates have not been obtained for each of these formations it is difficult to establish their original duration. Inferences can be made, however, from the sedimentary complexity and development of these deposits, along with the floral evidence, to determine their relative duration.

The Minginish Conglomerate Formation probably represents the most mature sedimentary environment preserved within the Skye Lava Field as its deposits are not solely erosional or weathering features but reflect more evolved depositional environments and sedimentary processes (Williamson and Bell 1994). The cyclic fluvial deposition pattern of conglomerates-sandstone-siltstone observed within the Allt Geodh' a' Ghamhna Member, and to a lesser extent the Allt Mor Member, indicate that this palaeoenvironment developed over a longer interval relative to other sedimentary formations (Williamson and Bell 1994). The presence of fossil floras that represent a broad range of plant types indicate that this environment must have been stable for a moderate period of time to facilitate their colonisation and development into relatively mature ecosystems (Jolley 1997).

The Minginish Conglomerate Formation is however, better constrained temporally than the other sedimentary formations with the Skye Lava Field based on its relationship with the Rum Central Complex. The lower age estimate of the Skye lava field is based on the clast composition within the Minginish conglomerates. Several of the conglomerates within the Allt Mor and Allt Geodh' a' Ghamhna members contain many of the rock types of the Rum Central complex and their isotopic composition is comparable (Meighan et al. 1981, Williamson and Bell 1994). It is important to note that the study by Meighan et al. (1981) was published only as an abstract so full details regarding the geochemistry of the clasts in both the Rum Central Complex and the Minginish conglomerates is limited. Since the lower age estimate of the SLG is based solely on the presence of these clasts and their suggested origin from the Rum Central

Complex, the validity of these results is questionable. It is likely that these clasts were derived from the unroofed Rum Central Complex and that the SLG began its development at 60.53 ± 0.08 Ma, but additional details of the original study of Meighan et al. (1981) must be published in full or a new study must be implemented to confirm this assertion.

Palynological evidence has also been used to date the interbasaltic sequences and SLG as a whole. Jolley (1997) suggested an age of 58.23-57.99 Ma for the SLG based on the similarities of the palynomorph assemblages of Skye to offshore West Shetland Basin deposits of late Selandian (~59 Ma) to the early Thanetian age (~58 Ma). Abundant and distinctive palynomorph taxa from the interbasaltic sequences on Skye, Canna and Rum include *Inaperturopollenites hiatus*, *Tricolpites*, *Retitricopites*, *Momipites*, *Laevigatosporites haardi* and *Sequoiapollenites polyformis* (Jolley 1997). These taxa were regarded by Jolley (1997) to be typical of the late Seladian and Thanetian interval. These taxa do, however, occur throughout the BTVP and are indeed common components of the sedimentary sequences (Jolley 1997). The occurrence of these taxa therefore suggests they are not necessarily useful for zonation.

This dating method indicates that the entire Skye Lava Field formed within 0.28 m.y. interval, which is in contrast to the dating by Hamilton et al. (1998), which suggested an interval of 1.6 m.y. This considerably shorter interval for the development of the entire SLG also seems unlikely as magma production rates would have to be an order of magnitude greater (Hamilton et al. 1998). It therefore seems more likely that radiometric dates are far more reliable than the palynological estimates of Jolley (1997) as they are more consistent with the chronological evolution of the province as a whole and are considered here as a more reliable age estimate for the Minginish Conglomerate Formation and the floras it contains.

2.6 Stratigraphy and sedimentology of the Paleocene fossil plant beds of Skye

2.6.1 Northern Skye

The Palagonite Tuffs of northern Skye represent some of the earliest and most explosive periods of volcanic activity on Skye. The tuffs were deposited on Jurassic rocks in an aqueous environment (Anderson and Dunham 1966). The presence of agglomerates and widespread tuff deposits indicates periods of explosive volcanism, which is common feature of the early phases of volcanism of the BTVP (Anderson and Dunham 1966, Williamson and Bell 1994, Emeleus et al. 1996, Emeleus 1997). Plant remains consisting of *Ginkgo* and indeterminate conifers are present within some of the tuff horizons (Anderson and Dunham 1966), indicating the establishment of plant communities. These plant remains, which are stored in the National Museums of Scotland, Edinburgh were studied, but due to poor labelling it was difficult or impossible to determine the locality from which they were collected. Additionally, most of the specimens were of low quality, and could therefore provide little taxonomic or climatic value, and for these reasons they were not used in this study.

2.6.1.2 Glen Osdale

Sequences of conglomerates, sandstones and mudstones are preserved below the Bracadale Lava Group (Anderson and Dunham 1966) and are indicative of braided river deposition similar to that of the Minginish Conglomerate Formation of west-central Skye. Fossil leaves were collected as part of this project from a section in the Glen Osdale sedimentary sequence at NG 232 238 (Figure 2.5). The plant-bearing section is exposed on the north side of the river next to a waterfall (Figure 2.6-a). This sequence is composed of sandstone units interleaved with a relatively thin (10-15 cm) siltstone units, the overall thickness of the sequence is approximately 182cm (Figure 2.6, 2.7). The base of the sequence is not exposed and further attempts to locate the base of the sequence along the River Osdale were unsuccessful.

The sedimentary sequences sampled at Glen Osdale appear to reflect fluvial deposition, with the sandstone units representing higher energy flood regimes while the silts and shales probably reflect waning energy levels and overbank deposition. The occurrence of plant remains throughout the sequence suggests the area around this site of deposition was vegetated. The possible rootlets and plant stems within some of the beds indicate that these flooding surfaces were vegetated after deposition. The fossilised leaves collected from Glen Osdale are poorly preserved and mostly highly fragmented. The leaves occur as isolated fragments or less frequently in low density clusters. They are preserved primarily on the mud laminae within the siltstones but several are preserved within the silt layers but are more poorly preserved.

Figure 2.6. a) Waterfall over the interbasaltic sediments of Glen Osdale, sediments and fossil plants sampled adjacent to waterfall. b) Upper part of the Glen Osdale sedimentary sequence below contact between overlying basalt flow 1, massive bedded fine-grained micaeceous sandstones, 2, shales with carbonised plant fragments, 3, overlying lava flow of the Bracadale Formation.

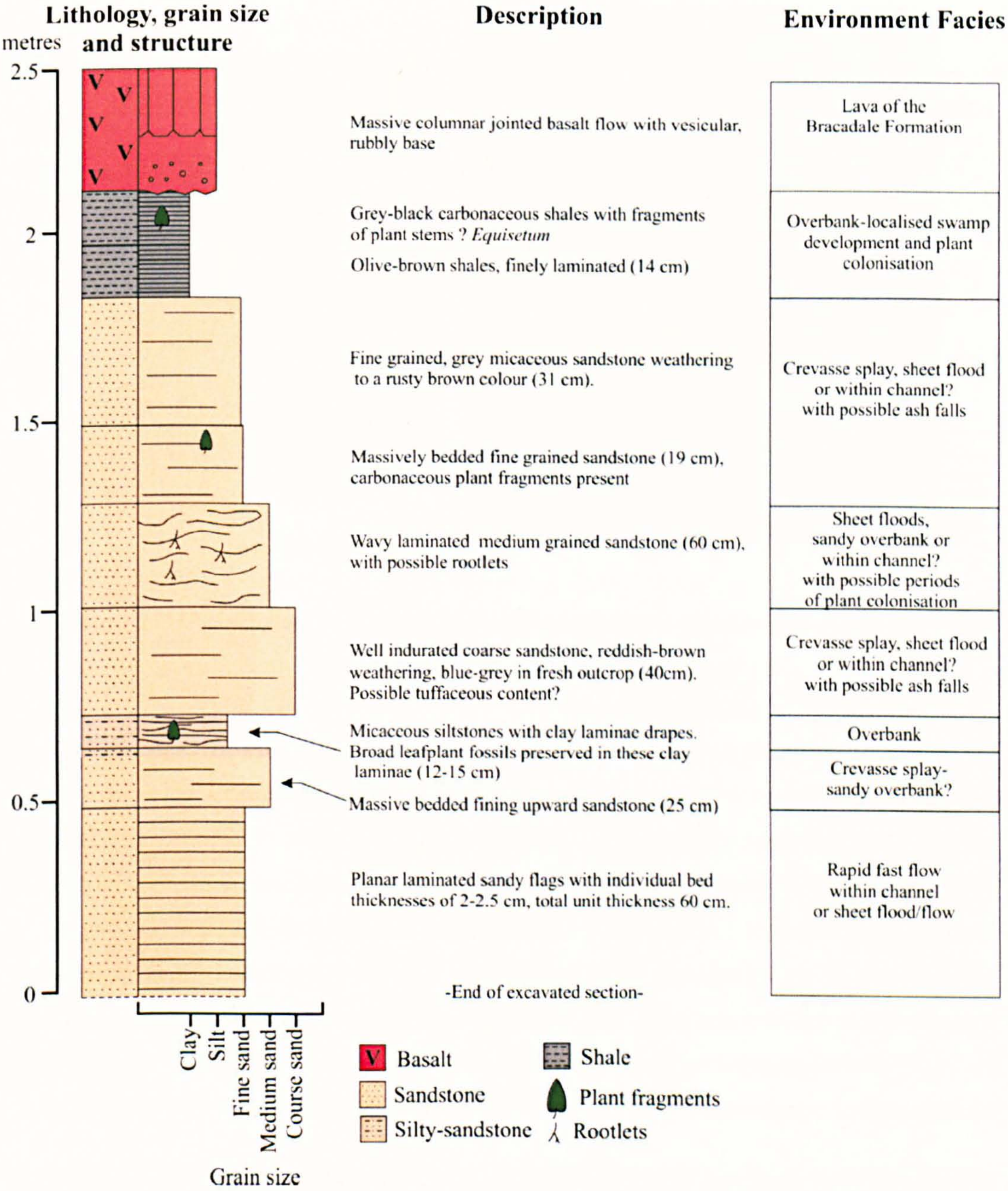

Figure 2.7. Sedimentary log of the Glen Osdale fossil plant locality (NG 232 438). Log taken by Lyall Anderson (National Museums of Scotland, Edinburgh) during collecting trip for this study.

2.6.2 Minginish Conglomerate Formation

The oldest sedimentary sequence in the Skye Lava Group, the Minginish Conglomerate Formation of west central Skye, is preserved between the Bualintur and Crucachan Lava Groups (Figure 2.9, 2.10). Three members of the Minginish Conglomerate are exposed: the Culnamean, Allt Geodh' a' Ghamhna and Allt Mor members all outcrop between Loch Brittle and Eynort (Figure 2.8). The Allt Geodh' a' Ghamhna and Allt Mor members are the most complete sedimentary sequences on Skye and are typically 10-15 m thick (Williamson and Bell 1994). This formation has also provided the majority of the fossil plant remains used in this study.

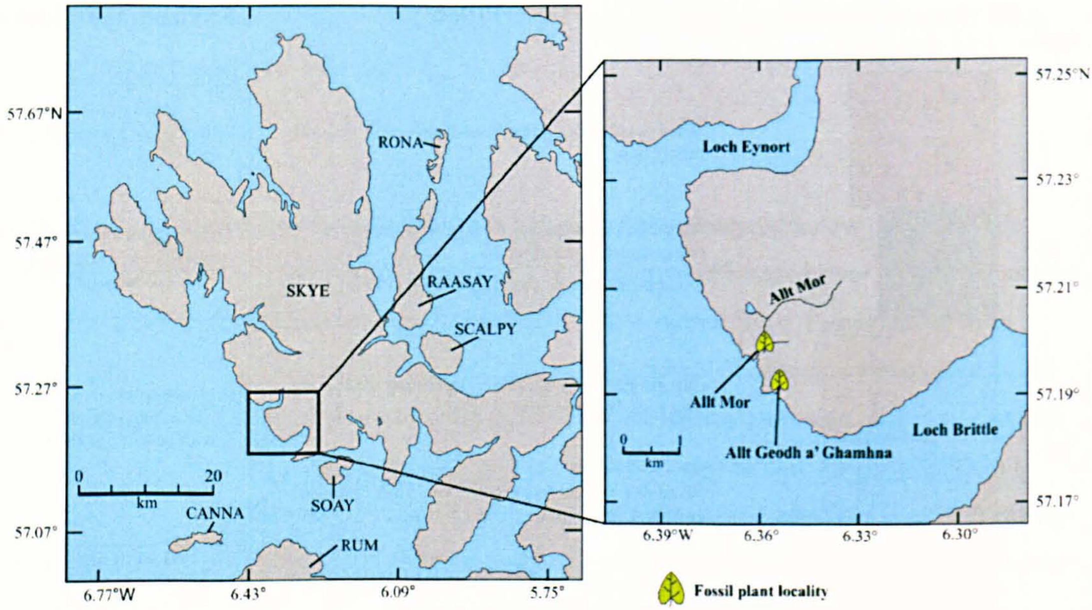

Figure 2.8. Sketch map showing the fossil localities in the Minginish Conglomerate Formation of west-central Skye.

2.6.2.1 Allt Geodh' a' Ghamhna Member

Packages of massive conglomerates, lenticular sandstone bodies and localised silts and coals are present. These represent cyclic deposits that have been interpreted as braided river deposits, with the conglomerates being deposited by high-energy flow regimes (Williamson and Bell 1994). The lenticular sandstone units represent waning energy levels resulting in lateral sheet and channel fill deposits. Localised silts and coals indicate that floodplain ponds and swamp environments developed adjacent to the braided river system. Approximately three cycles are apparent within the 15 m sequence, with a lower conglomerate and lenticular sandstone forming the lowest packet; a second conglomerate, sandstone and thin coal overlying this, followed by a third package of conglomerate with thin coals and sandstones (Williamson and Bell, 1994).

Fossil leaves from sediments within this sequence are stored in National Museums of Scotland, Edinburgh and were used in this study. The leaves were collected by Jason Hilton in 2004. The stratigraphy of the Allt Geodh' a' Ghamhna Member was documented by Williamson and Bell (1994) and is figured in 2.9. The leaves are preserved in buff-grey silt/sandstones, which probably reflect higher energy overbank deposition. The leaves are poorly preserved and typically occur as isolated, fragmentary specimens.

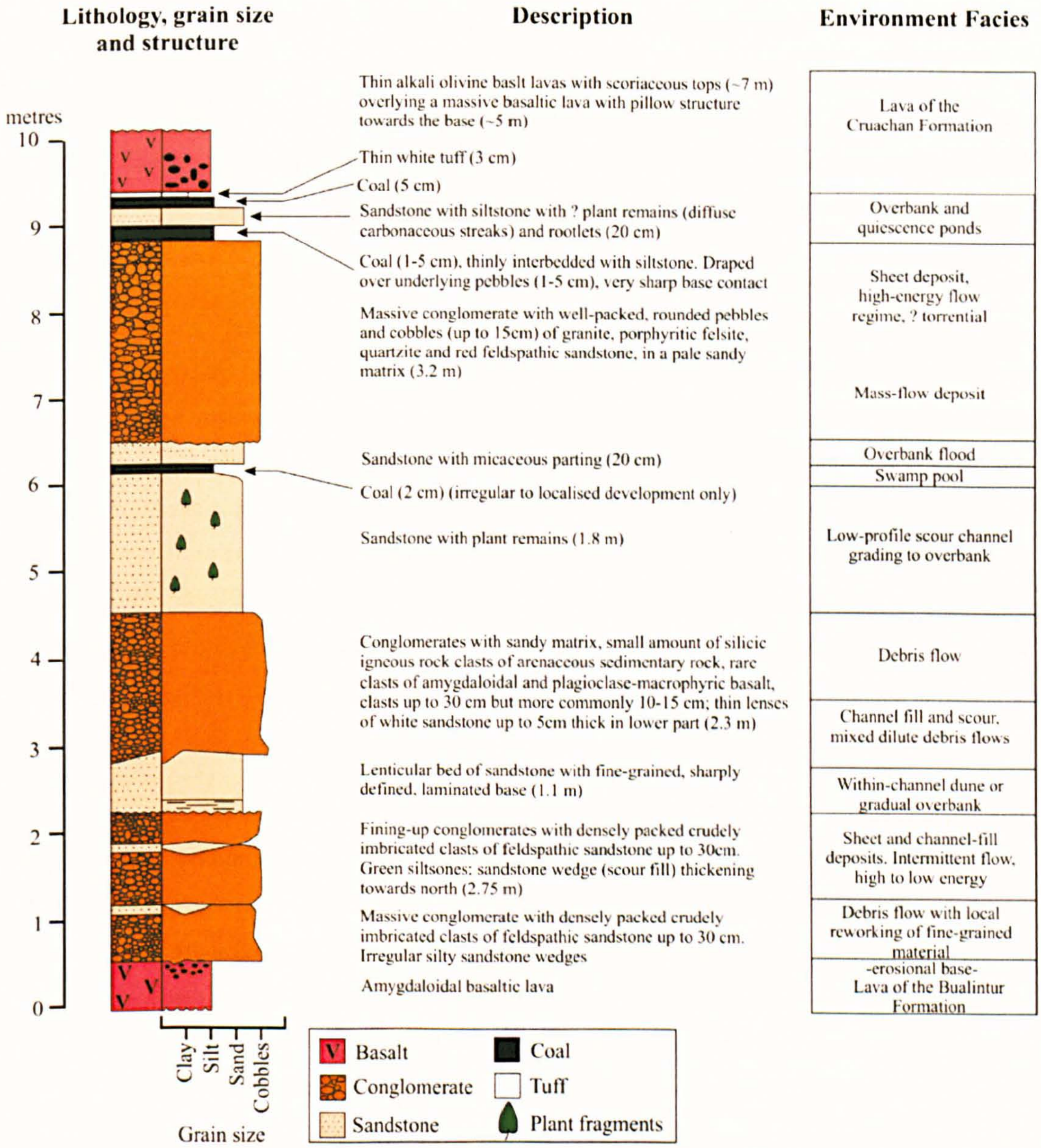

Figure 2.9. Sedimentary log of the plant-bearing sediments of the Allt Geodh' a' Ghamhna Member (NG 369 197). Redrawn from Williamson and Bell (1994).

2.6.2.2 Allt Mor Member

The Allt Mor Member is exposed in the Allt Mor ravine by the Allt Mor river (NG 366 204) in west-central Skye (Figure 2.8). The sedimentary sequence consists of conglomerates, sandstones and siltstones, which are preserved between the Bualintur and Cruachan Lava Formations (Williamson and Bell 1994). Williamson and Bell (1994) carried out an extensive examination of the sedimentary strata present within the Allt Mor ravine. They indicated that the sedimentary sequence is similar to that of Allt Geodh' a' Ghamhna Member 900 m to the SE, but displays more complex interbedding relationship of both the sedimentary rocks and basaltic flows (Williamson and Bell 1994).

The strata exposed within the ravine have been divided into three sections by Williamson and Bell (1994). Presented here is a brief summary of these three sections; the first two sections are from details within Williamson and Bell (1994). The third section, which contains the plant fossils, is based on details from Williamson and Bell (1994), but the beds that contain the plant fossils are described based on personal field observations (Figure 2.10).

The first section exposed on the south-east side of the ravine (NG 366 205) is composed of two conglomerates. The first type is matrix supported and is massively to crudely graded and the second is clast supported with a highly variable structure (Williamson and Bell 1994). These conglomerates are interleaved with fine grained pale-brown sandstones with an overall thickness of 6-7 m (Figure 2.11) (Williamson and Bell 1994). Both the sandstones and conglomerates pinch out towards the west of the ravine and are replaced by a lateritic surface (Williamson and Bell 1994). A unit of red arkosic sandstone of 1-1.5 m thickness is separated from the above mentioned strata by thin (9m thick) basaltic lava flows (Williamson and Bell 1994). These arkosic sandstones are exposed on the opposite side of the ravine and are laterally continuous and show weak cross-bedding with foreset beds inclined 20-30° to the north or north east (Williamson and Bell 1994).

The second section is exposed further upstream within the ravine (towards the north-east). Red-brown sandstone of 1-2 m thickness overlies conglomerates (Williamson and Bell 1994). These conglomerates are interbedded with thin beds of coarse-grained sandstones that are often pebbly. Small lenses of sandstone occur within the conglomerate and these show lenticular bedforms with cross bedding that dips towards the north. The composition of these two conglomerates is quite different, the lowermost is 4 m thick and is mixed-matrix and clast-supported. The second conglomerate (upstream) is 2 m thick with clasts of red arkosic sandstones, greenish siltstones and shale but with clasts of granophyres and amygdaloidal basalt. The size of these clasts is also quite variable, ranging from pebble to boulder sized fragments. The composition, size range and sorting of this conglomerate is typical of the conglomerates of the Allt Geodh' a' Ghamhna Member fragments (Williamson and Bell 1994).

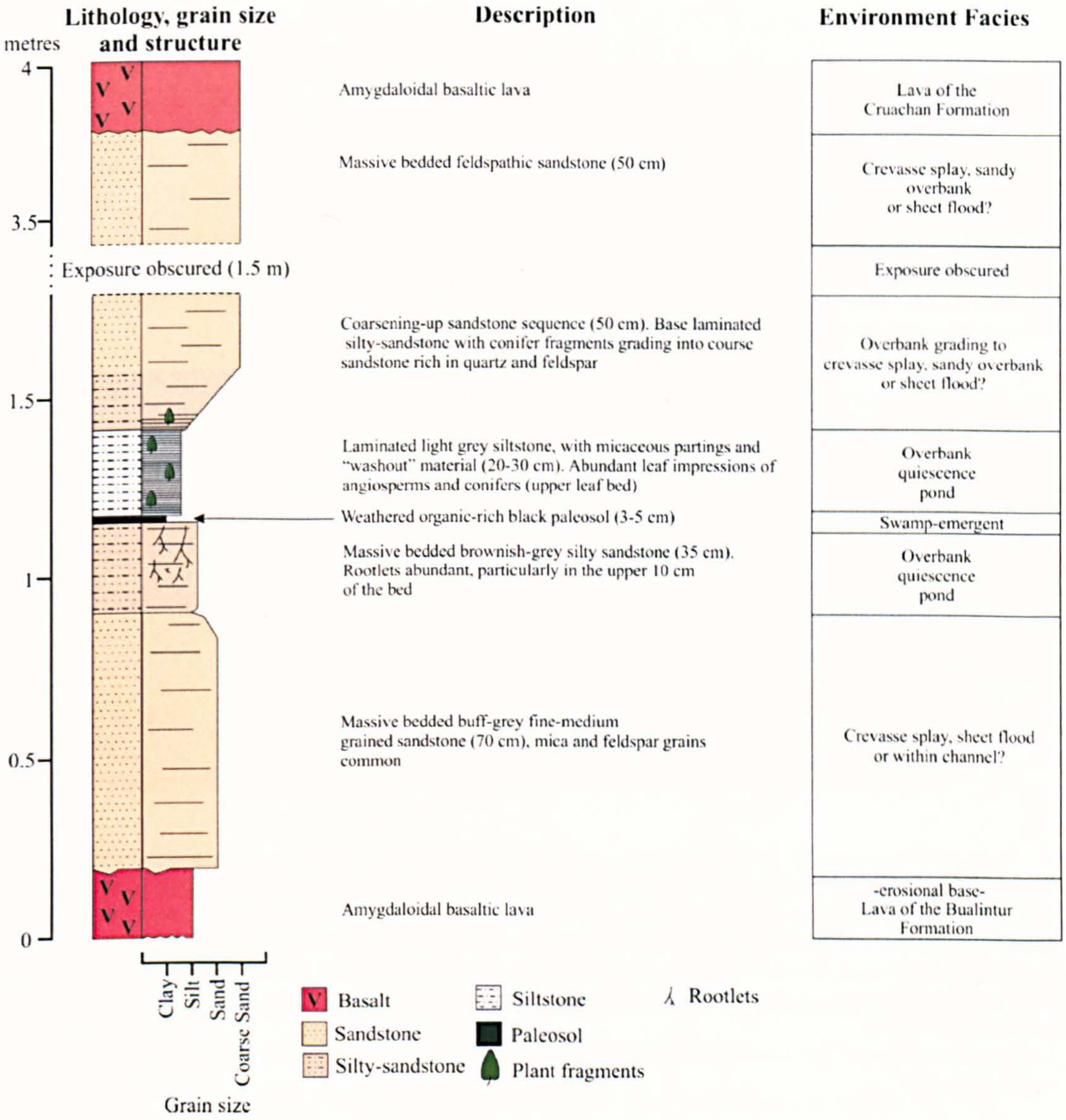

Figure 2.10. Sedimentary log of the plant-bearing sediments of the upper leaf bed of the Allt Mor Member (NG 367 206). Log taken by Jon Poulter during collection trip for this study.

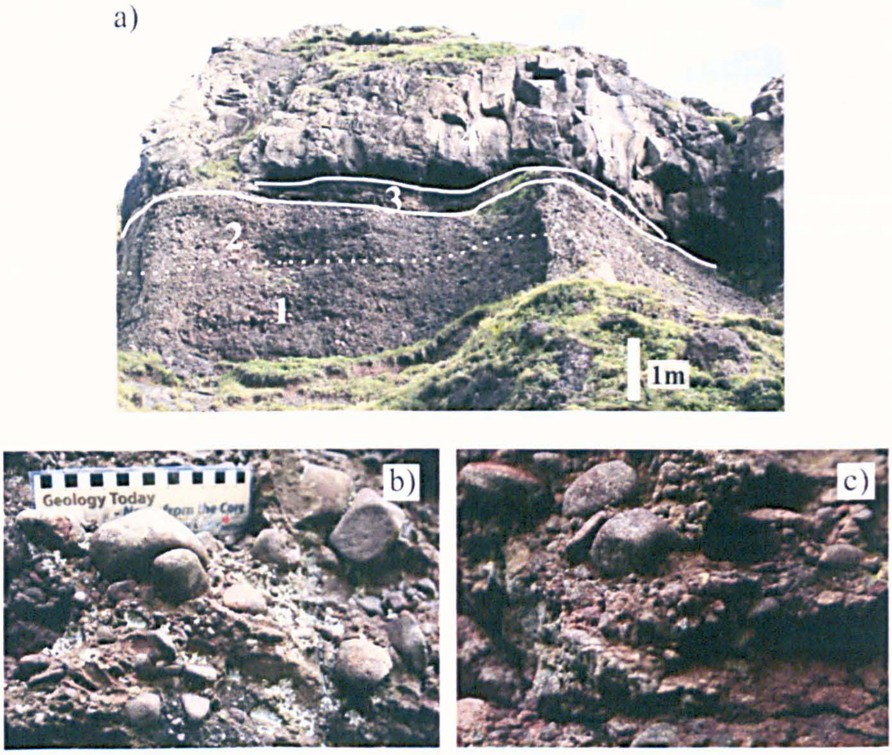

Figure 2.11. Section 1 of the Allt Mor ravine displaying relationships of conglomerates, sandstones and overlying lava flow. a) 1, Mixed clast and matrix supported conglomerate with variable clast sizes ranging from 1-30 cm 2, Conglomerate grades into solely clast supported, 3, brown medium-grained sandstone, 4, basaltic lava flow of the Cruachan Lava Formation. b) Conglomerate, both clast and matrix supported, scale 17 cm. c) matrix supported conglomerate, matrix is fine-medium-grained sandstone.

Figure 2. 2.12.

The third section is exposed further upstream within the ravine and is similar to those previously mentioned with alternating sedimentary beds and lava flows. The most downstream part of the third section is composed of thin conglomeritic sandstone, overlain by a 15 m thick lava flow, which is in turn overlain by conglomerates, sandstones and pebbly sandstone fragments (Williamson and Bell 1994). The uppermost exposure of the Allt Mor Member is composed of a ~12 m thick unit of fine-medium grained silty, pink feldspathic sandstone. Siltstones are present at the waterfall section (NG 367 206) and these contain leaf impressions and compressions, woody fragments and roots (Figures 2.13, 12.14). A large 3-4 m fallen block of basalt is preserved within a section of these siltstones. Below this fallen block the siltstones show deformation under its weight, Williamson and Bell (1994) report that plant fossils, including leaf impressions are preserved in the silts below the fallen block (Figure 2.12-a). Due to poor access and high water levels during the periods of collection fossils were not collected from below the block. Laterally equivalent siltstones however, contained rich and well preserved leaf impressions and large woody fragments (Figure 2.12-b,c).

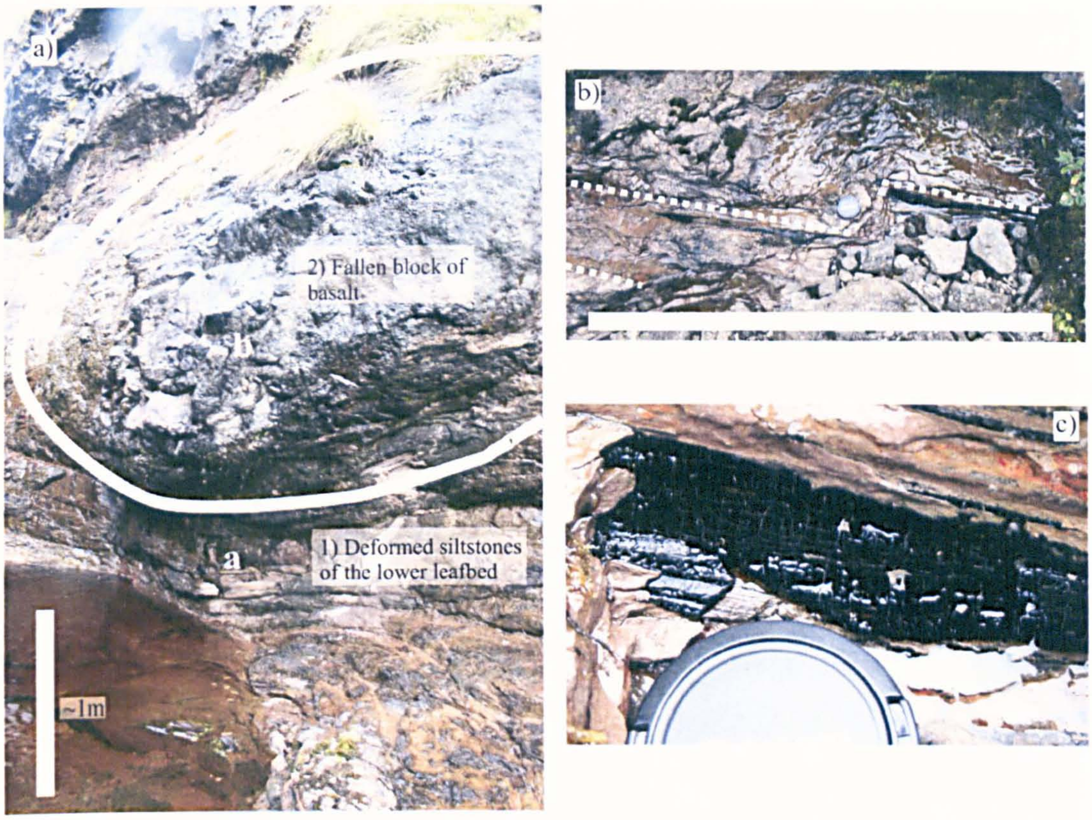

Figure 2.13. a) 1, deformed siltstones containing abundant fossil leaves, 2, fallen block of basalt that has deformed the underlying siltstones. b) Siltstones of the lower leaf bed with large woody fragment (dashed lines represent exposed outline) of a trunk or branch. c) Close up of the large woody fragment, showing the carbonised structure of the wood. Lens cap 6 cm.

The siltstones and sandstones preserved below the waterfall section at NG 367 206 were sampled and measured more thoroughly and provided the bulk of the leaves that were examined for this study. Several field seasons between 2002-2009 were carried out to collect the leaf fossils, with the 2002 collection by Jane Francis, Jason Hilton and Helena Eklund providing the majority of the leaf specimens used in this study. Two beds have provided the majority of the leaf fossils and these are termed the lower and upper leaf beds. The lower leaf bed (Figure 2.12-b) is the lateral equivalent of the siltstone units below the fallen block shown in figure 2.12-a. The dark grey-brown siltstones of the lower bed are finely laminated and on certain lamina are crowded with leaf impressions, representing extensive lateral leaf mats. Other laminae, however, contain little leaf material. Carbonised woody fragments are also abundant including a large, trunk or branch that is approximately 2 m long (Figure 2.12-b). The vertical extent of this sequence is difficult to determine as modern overburden obscures the top of the exposure.

The upper leaf bed consists of grey, black or buff finely-laminated siltstones that contain abundant and well preserved plant fossils, particularly leaf impressions. The stratigraphy of the upper leaf is better known as more of this vertical extent is exposed (Figure 2.10, 2.11, 2.13).

Figure 2.14. a) Upper leaf bed and overlying lava flow, 1, siltstones and sandstones of the upper leaf bed, 2, overlying basalt of the Cruachan Lava Formation. Yves Candela right and Jon Poutler left. b) Siltstones and sandstones above the upper leaf bed, scale bar = 17 cm. c) 1, laminated siltstones containing abundant plant fossils, 2, coarsening-up sequence of siltstones and sandstones, plant fossils restricted to lower 10 cm of the bed, 3, fine to medium grained sandstones , plant fossils rare. Lens cap = 6 cm. d) Contact between Cruachan Lava Formation and uppermost bed of the Allt Mor plant beds. Dashed line denotes the uneven contact between the feldspathic sandstone and overlying basaltic lava flow. Lens cap = 6 cm.

The sedimentary sequence of the lower and upper leaf beds is interpreted as reflecting pond deposition, where overbank floods deposited the sediments into a natural hollow within the lava surface. The conglomerates, pebbly sandstones and feldspathic sandstones present in sections 1 and 2 of the Allt Mor Ravine have been interpreted by Williamson and Bell (1994) as being deposited in a braided river system, which flowed from the southeast to northwest following a natural palaeovalley. The high proportion of mica and feldspar within these clastic sediments suggests they were derived from local Torridonian sequences and the unroofted Rum Central Volcano (Williamson and Bell 1994). Vegetation colonised the margins of the rivers, ponds and floodplains and their remains were transported laterally by flood waters into the pond deposits. The fossil leaf deposits at Allt Mor are probably a combination of allochthonous and autochthonous elements, being derived from both local vegetation and plants across the palaeovalley. The pond deposits at Allt Mor appears to have developed into a swamp for a short interval because a organic rich palaeosol is present. The silty sandstone below this bed contains abundant rootlets, which indicates that the surface became vegetated, and their remains contributed to the development of the palaeosol.

The fossil leaves from Allt Mor vary considerably in their abundance on each laminae, and their overall preservation and quality. Details about the overall quality and preservation of the leaves are discussed in more detail in Chapter 3 (see section 3.5).

2.8 Summary

The British Tertiary Volcanic Province represents one of the best studied large igneous provinces in the world and thus its development and evolution are well understood. Igneous activity within the BTVP began in Northern Ireland at ~62 Ma (Ganeørod et al. 2010), which was followed by the development of lava fields in the Inner Hebrides between 61-60 Ma. The development of the extensive lava field of Antrim, Skye and Mull occurred rapidly within an interval of 1 to 2 million years. Volcanic central complexes developed in relatively short periods ~1 million years. Igneous activity was not continuous however, as sedimentary deposits are interbedded within the lava sequences. The composition of the sedimentary strata indicates a variety of depositional environments developed on the lava surfaces. Within some of these sedimentary sequences fossil plant remains are preserved. These remains indicate that during volcanically quiescent intervals vegetation colonised the lava surfaces and developed into rich plant communities. Most notable of these plant bearing units at Ardtun Head, Mull; Glen Osdale, northern Skye; and Allt Mor and Allt Geodh' a' Ghamhna, west-central Skye. All these localities are characterised by fluvial and lacustrine deposition associated with braided river systems, floodplain deposits and localised swamp development. Fossil plant remains are typically concentrated in the finer grained sands, silts and shales that represent localised lakes, ponds and pools that developed on the lava surface. Vegetation accumulated in these pools from plants growing around them, or were washed in by flood events. Radiometric dating and stratigraphic relationships within the Skye Lava Group have enabled relatively high resolution dating of the fossil leaf beds of the Minginish Conglomerate Formation. The radiometric dating estimates for the west-central Skye floras have provided an age estimate of 60.28 ± 0.45 Ma. This dating indicates that floras of Skye are mid Paleocene in age.

Chapter 3: Leaf collections and angiosperm morphotypes

3.1 Introduction

The fossil leaves from the plant-bearing sediments of Skye provide an opportunity to determine the floral composition of this region during the Paleocene. Leaf fossils have been collected from three localities on Skye: Allt Geodh' a' Ghamhna, Allt Mor and Glen Osdale. These localities have provided new collections of plant fossils, which are described for the first time in this study. This chapter presents the fossil leaf collections used in this study and the techniques used to describe and categorize them. Details regarding the number system used to catalogue the specimens, the broad taxonomic composition of the floras and the techniques used to begin the description process are outlined. The quality of the specimens, including details of their fragmentation, completeness, venation quality and size are presented. The concepts of angiosperm leaf classification and description and how this can be applied to fossil floras are outlined. The angiosperm leaf morpotypes identified from Skye are presented with detailed descriptions. Each morphotype description includes the specimen numbers, diagnosis and comparison with previously described fossil taxa where possible. A discussion of the morphological characteristics and variability, and its similarities to other fossil and modern floras is included.

3.2 Numbering of specimens

Specimens used in this study are housed at the National Museums of Scotland, Edinburgh. All specimens accessioned at the National Museums of Scotland are numbered. The numbering system is consistent and contains the year in which the specimen was accessioned in the collection, and to which series it belongs in the specimen catalogue followed by its own number. Each specimen begins with the letters NMS.G, which refers to the National Museums of Scotland Galleries. This is then followed by the year the specimen was accessioned e.g. NMS.G.2004, followed by second number which denotes the specimens collection number within the catalogue of specimens e.g. NMS.G.2004.29. This number is then followed by the sample number e.g. NMS.G.2004.29.083. Some rock specimens contain several individual leaf fragments. When this is the case for this study each is provided with a letter at the end of the specimen number e.g. NMS.G.2004.29.083-a. Not all individual leaf fragments were given specific letters within this study, including the conifer fragments and the highly fragmented and poorly preserved angiosperm specimens.

The museums catalogue of specimens contains the details of the locality from which the specimens were collected including, geographical and geological information, and taxonomic information where possible.

A portion of the NMS collection of fossil leaves from Skye is un-accessioned; this refers to the lack of placement of these specimens in the museum's catalogue. These specimens can be manipulated more readily i.e. spilt to provide more specimens. Since these specimens were to be re-examined several times during the course of this study it was decided that they should remain un-accessioned until the end of the study period. Un-accessioned specimens were given a different numbering system; firstly the locality name is stated as two letters followed by NA (not accessioned) e.g. AM.NA (AM = Allt Mor, Skye), followed by the slab number and individual fossil specimens were given letters e.g. AM.NA.004-c. Thirteen samples were in the process of being accessioned but were not officially added into the museum catalogue. These samples were denoted firstly by ACC, which refers to near-accessioned status followed by the sample number e.g. ACC.001. A third series of samples were collected by Jon Poulter, Yves Candela, Edward Shaw and Daniel Bradshaw in two collecting seasons in 2008 and 2009. These specimens were collected from the upper leaf bed of Allt Mor (see Chapter 2, section 2.6.2.1). These specimens were numbered firstly by the locality, followed by the year of collection, the sample number and a letter to denote specific leaf specimens e.g. AM.NA.08.001-a. These specimens will be accessioned at a later date, and given the standardized National Museums of Scotland specimen numbers.

3.3 Specimen Information

3.3.1 Allt Mor

The collection of fossil plants from the Allt Mor locality comprises 379 fossil-rich samples, and approximately 2572 leaf fragments. Of these specimens, 1158 represent dicotyledonous angiosperm leaves and the remaining 1414 represent conifer shoots. The vast majority of these specimens were either individually photographed or drawn from the hand specimens. The overall composition of the Allt Mor flora is displayed in Figure 3.1.

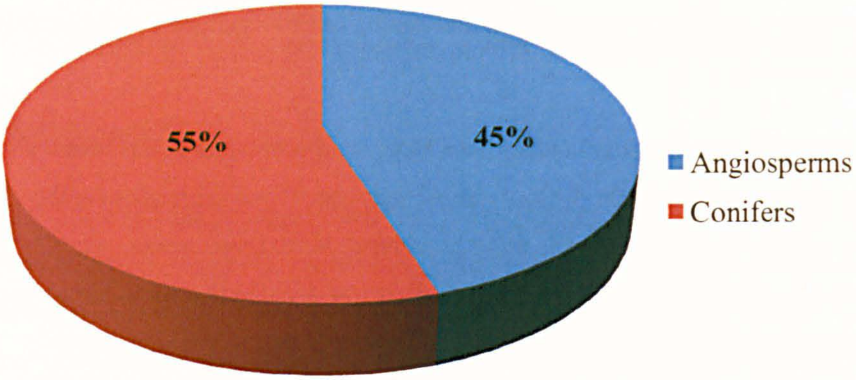

Figure 3.1. Percentage of angiosperm and conifer fossils in the Allt Mor collection.

The angiosperm leaves and conifer shoots are preserved as impressions or compressions within grey, buff or orange siltstones and more rarely in fine grained buff sandstones. They occur either as scattered fragments, small clusters or as leaf mats (Figure 3.2). Some laminae contain an abundance of floral remains, while others are devoid of leaf fossils. Wood and bark fragments are relatively common, roots are relatively rare and are typically restricted to specific horizons (see Chapter 2, Figure 2.10). The floral composition of each slab is variable; some contain a mix of angiosperm and conifer fragments, while others are dominated by one of these types (Figure 3.2).

Angiosperm cuticle has not been observed on the specimens which may be a result of the intense heating caused by the overlying basaltic lava flows. Conifer cuticle is also appears absent and the majority of the specimens are coalified, but some do show signs of potential cuticular impressions within the sediment. The overall quality of the specimens is fair, the angiosperms often have their overall leaf form, margin and venation patterns preserved. Most leaf specimens have primary and secondary venation preserved, and a high proportion have tertiary venation preserved. Higher order venation preservation, however, is uncommon.

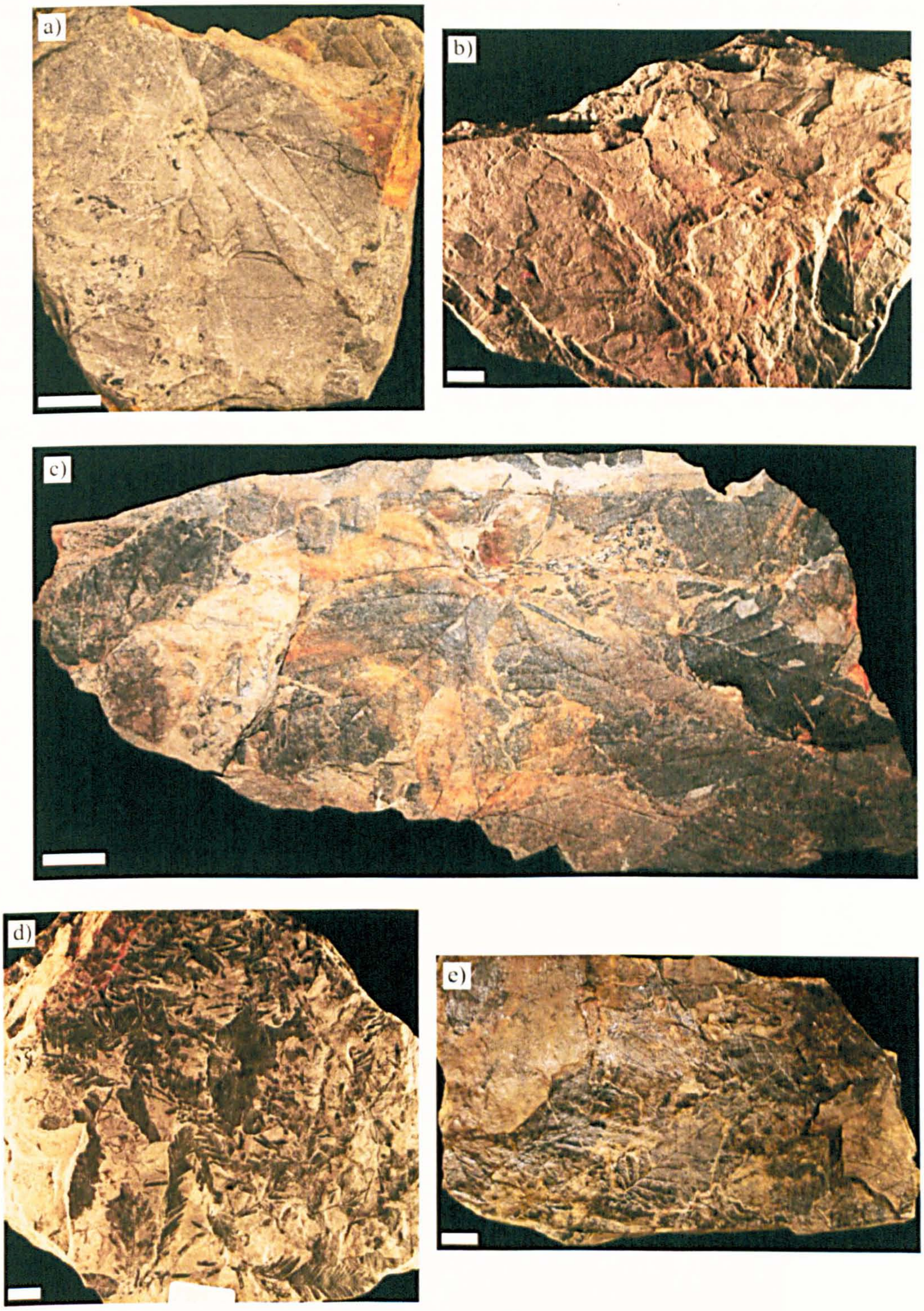

Figure 3.2. Examples of specimens from the Allt Mor plant assemblage of Skye, showing differing preservation patterns. a) Example of scattered fragmented leaf specimens (ACC.010), b) example of clustered arragement of angiosperm leaf specimens (NMS.G.2004.29.055), c) example of leaf-mat composed primarily of angiosperm leaf fossils (AM.NA.001), d) example of a conifer dominated sample (NMS.G.2004.29.008), e) example of a lamina dominated by angiosperm leaves (AM.NA.084). Scale bars = 1 cm.

3.3.2 Allt Geodh' a' Ghamhna

The Allt Geodh' a' Ghamhna locality is small and has yielded only seven samples, which were collected by Jason Hilton in 2004. The collection includes eight angiosperm leaf specimens and two wood fragments. The floral remains are preserved in fine to medium-grained buff sandstones that may correspond to the sandstone unit that is between the second and third conglomerate units of the Allt Geodh' a' Ghamhna Member (see Chapter 2, Figure 2.9). The angiosperm leaves are poorly preserved and their overall form, margin and venation patterns are unclear (Figure 3.3). It is therefore difficult to establish their taxonomic affinity. Conifer shoots or fern fronds have not been found in the limited collection from Allt Geodh' a' Ghamhna. Two wood fragments are present (AGG.006, AGG.007), their outer surfaces are relatively well preserved and show some details of their original structure (Figure 3.3). Due to the lack of internal preservation these wood specimens are not suitable for thin section to determine the taxonomic affinity or palaeoclimate signals they may have provided.

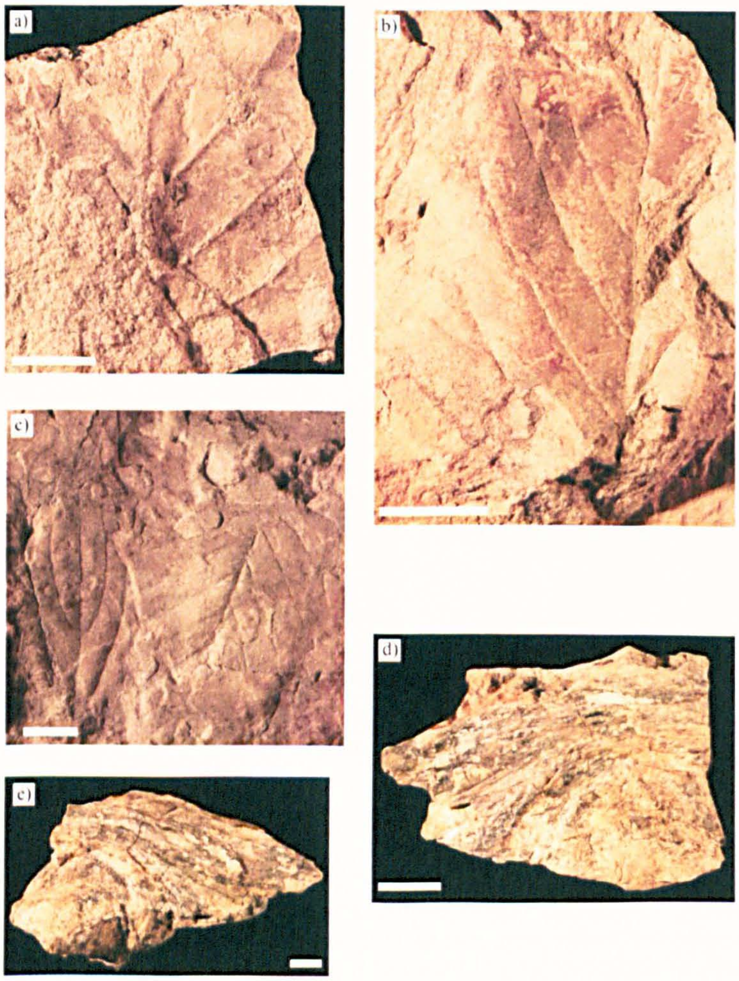

Figure 3.3. Examples of specimens from the Allt Geodh' a' Ghamhna plant assemblage of Skye. a) small angiosperm leaf fragment (AGG.003), b) angiosperm fragment (AGG.005), c) thrre angiosperm leaf fragments with better preservation (AGG.004), d) wood fragment (AGG.007), e) wood fragment (AGG.006). Scale bars = 1 cm.

This locality has provided 35 samples that contain fossil angiosperm leaf fragments, wood and roots. Forty three angiosperm leaf fragments have been identified, conifer shoots or fern fronds have not been found. The leaves are typically highly fragmented and are poorly preserved, but several specimens (e.g. NMS.G.2005.145.1, NMS.G.2005.145.13-a, NMS.G.2005.145.13-b) have reasonably well preserved venation and margins (Figure 3.4). The leaves are preserved in fine to medium-grained buff, brown or grey sandstones and in some cases are preserved in orange to red clay laminar (Figure 3.4). Wood fragments are present within the sediments of Glen Osdale and include a relatively large, ~25cm long log (Figure 3.4). The internal structure of the wood is not preserved so it is not suitable for thin sectioning. Roots are common in the sample from Glen Osdale but do not appear to be *in-situ*, but rather may have been transported into the assemblage (Figure 3.4).

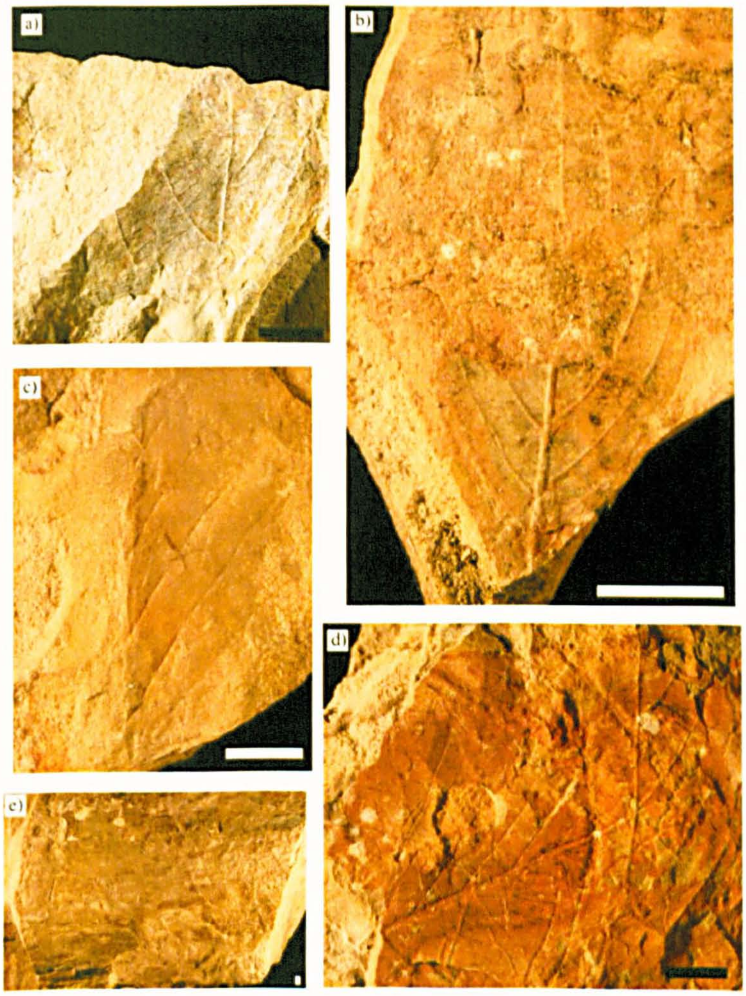

Figure 3.4. Examples of leaf specimens and fossil wood from Glen Osdale leaf assemblage of Skye. a) leaf fragment with well preserved venation (NMS.G.2005.145.1), b) well preserved angiosperm leaf (NMS.G.2005.145.7-b), c) poorly preserved leaf specimen typical of the Glen Osdale assemblage (NMS.G.2005.147.7), d) three angiosperm fragments preserved in red clay lamina (NMS.G.2005.145.14), e) fossilised wood that may represent a large branch or small trunk (NMS.G.2205.145.29). Scale bars = 1 cm.

3.4 Methods

The fossil leaves were photographed and drawn firstly to provide a record of the specimens within the collections and secondly, to help determine their morphology and taxonomic affinity. The procedures used in this study are described in the following section.

3.4.1 Preparation of the fossils

Un-accessioned specimens were cleaned where possible. Initial attempts of rinsing with water proved unsuccessful, as this often led to the disintegration of the friable siltstones. Leaf fragments were cleaned more successfully with fine brushes, but thick layers of soil could not be removed without damaging the specimens. Specimens that could be readily split to reveal more leaf fragments were split using a fine chisel and small hammer. The friable nature of the sediments meant splitting was relatively easy along fossiliferous lamina. This procedure led to the discovery of several exceptionally well preserved specimens, and increased the collection size significantly. Specimens that were partly obscured by overlying layers of sediment were exposed using an electric engraving tool.

3.4.2 Photography

The earliest phase of description and identification of the fossil leaves was done through digital photography of the specimens. The specimens were photographed at the National Museum of Scotland using a Digital SLR camera. All slabs were photographed and individual specimens were photographed if they were either well preserved, or possessed interesting morphologically details. Each slab and specimen was photographed with and without a scale bar for later reference and digital manipulation of the photographs.

Various lighting methods were tried to obtain the best results, and included ambient lighting, flash photography, and low angle lighting from lamps. Low angle lighting from side of the specimen proved the most successful method of capturing the details of the leaf specimens, but several lighting styles were used for the photography of each specimen.

The digital photographs were later manipulated using Corel Paint Shop Pro X. Each image was adjusted for contrast, brightness, saturation, shadows, highlights and mid tones to reveal the morphological characters of the leaf specimens.

3.4.3 Drawing

Graphical representation of the angiosperm leaf architecture was achieved digitally. Digital photographs of the specimens were imported into CorelDraw X5 for tracing of the leaf margin and venation patterns. The angiosperm leaf specimens venation and margins were traced by using either a mouse or a digital drawing tablet.

Tracing of the true leaf margin was done in a solid low point line; areas where the true margin is not preserved were denoted by a dashed line. The order of the venation was depicted by varying line the thicknesses. Primary venation has the thickest line, followed by secondary then tertiary etc. This facilitates the recognition of the vein patterns and vein orders within the drawing.

3.5 Preservation of the leaves

3.5.1 Fragmentation and specimen quality

The fossil angiosperm leaves of Skye represent foliar remains that have been shed from their parent plant and have either entered the site deposition directly or have been transported and deposited by water. Once at the site of deposition the leaves may become further degraded by detritivores and microbial decay. These combined processes can lead to fragmentation of leaves (Ferguson 1985). The level of fragmentation of the specimens may therefore be a useful indicator of transport. The influences and implications of transport and deposition on leaf fragmentation is discussed in Chapter 5 (see 5.3.2.3). The degree of fragmentation is also an indicator of the overall quality of preservation of the leaf assemblage.

To assess leaf fragmentation each specimen were placed into one of the three categories, adopted from Hayes (1999) (Table 3.1). The number of specimens in each fragmentation category for the Allt Mor collection is summarised in Figure 3.5.

Table 3.1. Angiosperm fossil leaf fragmentation categories and their description.

Fragmentation category	Description
Small fragment	Leaves that have no discernable margin or a very small percentage of margin preserved, and their original shape cannot be determined
Fragment	Leaves that have fairly clear margins preserved and partially preserved apex and base, although one of these may be missing
Almost complete	Leaves that are nearly intact, with a visible margin, base and apex

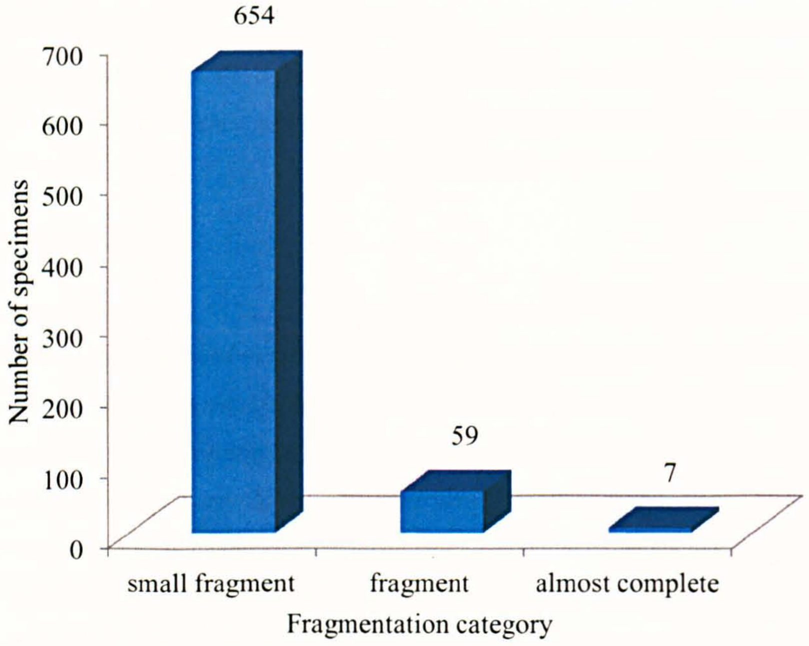

Figure 3.5. The degree of fragmentation of angiosperm leaves from the Allt Mor leaf assemblage, showing the number of specimens in three fragmentation categories.

The Allt Mor assemblage is dominated by small fragments, which account for 654 of the specimens (91%). The fragment category account for 59 (8%) of the specimens and only seven (1%) of the specimens are considered to be almost complete (Figure 3.6). This indicates that the angiosperm leaves of Allt Mor are highly fragmented. The cause of this fragmentation may be related to transport prior to deposition, but may also have arisen due to collecting and splitting of the samples in preparation for this study.

3.5.2 Leaf venation clarity

To assess venation preservation and clarity the leaf specimens were placed into one of five categories, which were adopted from Hayes (1999) (Table 3.2). These categories are based on the number of vein orders visible on the leaf specimen. The highest order vein preserved for that specimen is used to assign that specimen to the appropriate category i.e. a specimen with up to third order venation preserved is placed in the "fairly clear" category. The number of specimens in each venation clarity category for the Allt Mor collection is summaries in Figure 3.6.

Table 3.2. Definition of venation clarity categories of angiosperm leaves.

Venation clarity category	Number of vein orders preserved
Very clear	5
Clear	4
Fairly Clear	3
Fairly Unclear	2
Unclear	1

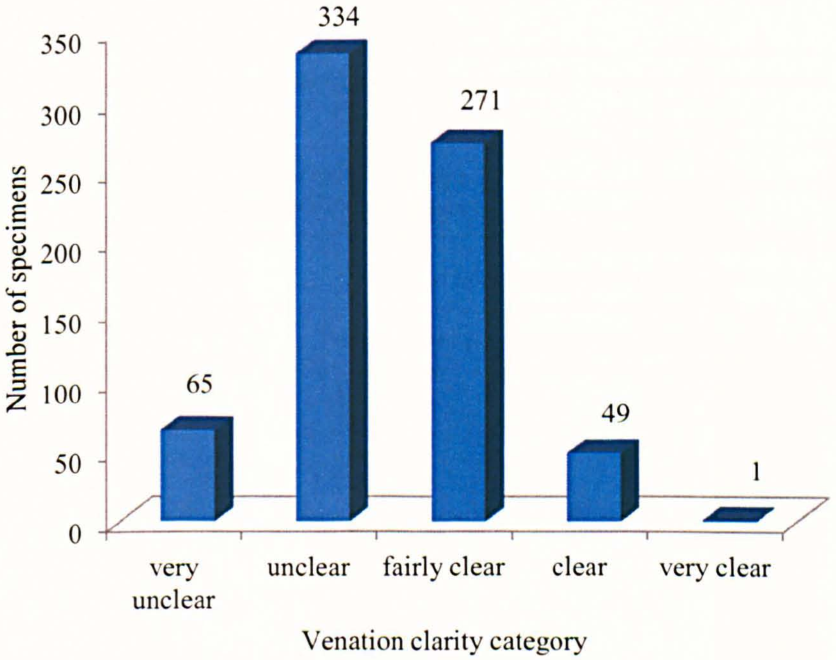

Figure 3.6. Venation clarity of the Allt Mor angiosperm leaves, showing the number of specimens in each of the five venation clarity categories.

The two categories with the largest number of leaf specimens are the "unclear" and "fairly clear", which account for 334 (46%) and 271 (38%) of the leaf specimens respectively (Figure 3.6). This indicates that the majority of the angiosperm specimens have up to second or third venation preserved. The "very unclear" category accounts for only 65 (9%) of the specimens (Figure 3.6), which indicates that leaves with very poor venation clarity are rare. Leaves with vein orders higher than three account for 7% of the collection, which indicates that only a small percentage of specimens have well preserved venation (Figure 3.6). Overall the venation clarity of the Allt Mor specimens appears to relatively good, as 45% of the specimens have third or higher order venation preserved, and should facilitate the recognition of the veins patterns, which in turn can be used to describe and identify the leaf specimens.

3.5.3 Leaf margin preservation

Angiosperm leaf margins have two important uses in palaeobotany, firstly, they can be used to identify the leaf types, and secondly, they can be for palaeoclimate analysis (see Chapter 6, section 6.2.1). To access the marginal preservation of the Skye angiosperm leaves the specimens were assigned to one of three categories that were adopted from Hayes (1999) (Table 3.3). The number of specimens in each venation clarity category for the Allt Mor collection is summarized in Figure 3.7.

Table 3.3. Margin preservation categories of fossil angiosperm leaves and their description.

Margin preservation category	Description
Margin absent	Leaf specimen has no margin preserved
Small percentage	Small portion of margin preserved, details of the margin unclear
Margin clear	Large proportion of the margin preserved and detailed morphology and apparent

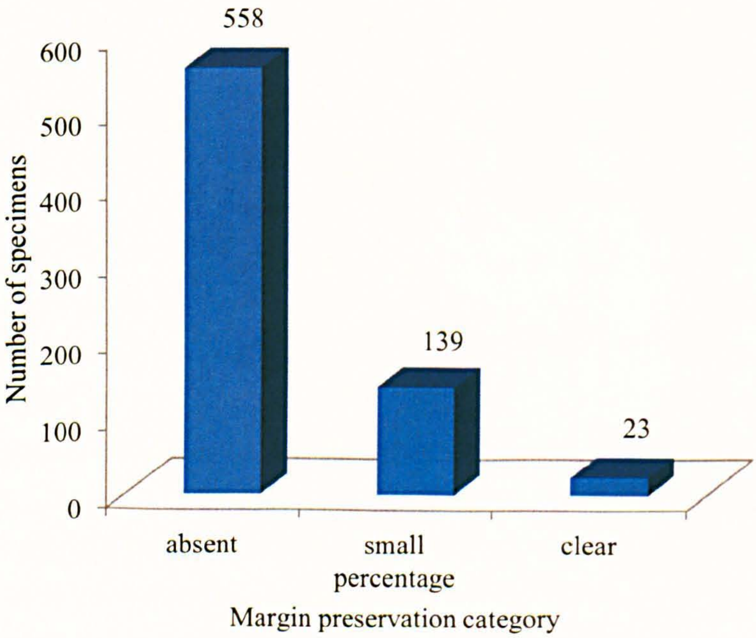

Figure 3.7. Margin preservation of the Allt Mor angiosperm leaves, showing the number of specimens in each of the three margin preservation categories.

Margin preservation is quite poor as 558 specimens (78%) of the specimens do not have margin preserved. Leaf specimens that do have margin preserved primairly have only have a small part preserved (19%) and only 23 specimens (3%) have well preserved, clear margins. This indicates that a large percentage of the specimens may be of limited use for palaeoclimate analysis as this leaf character is important for deciphering palaeoclimates (e.g. Wolfe 1979, Wing and Greenwood 1993, Wilf 1998). The implications of limited margin preservation and its potential impacts on palaeoclimate analysis are discussed in Chapter 6 (see sections 6.3.1, 6.4.4.2).

3.5.4 Leaf apex and base preservation

The apex and leaf bases of angiosperm leaves, like their margins, are useful for the identifcation of angiosperm leaves and can be used to decipher past climates. Determining the preservation of bases and apexes for the Allt Mor specimens is therefore of importance in this study. To access the preservation of leaf apexes and bases the Allt Mor angiosperm were assigned to one of three categories for base and apex preservation, adopted from Hayes (1999) (Table 3.4). The number of specimens in each apex and base preservation category for the Allt Mor collection is summarized in Figure 3.8.

Table 3.4. Apex and base preservation categories of fossil angiosperm leaves and their description.

Apex/Base preservation category	Description
Missing	Specimens apex or base not preserved
Incomplete	Specimens apex or base partially preserved
Complete	Specimens apex or base completely preserved

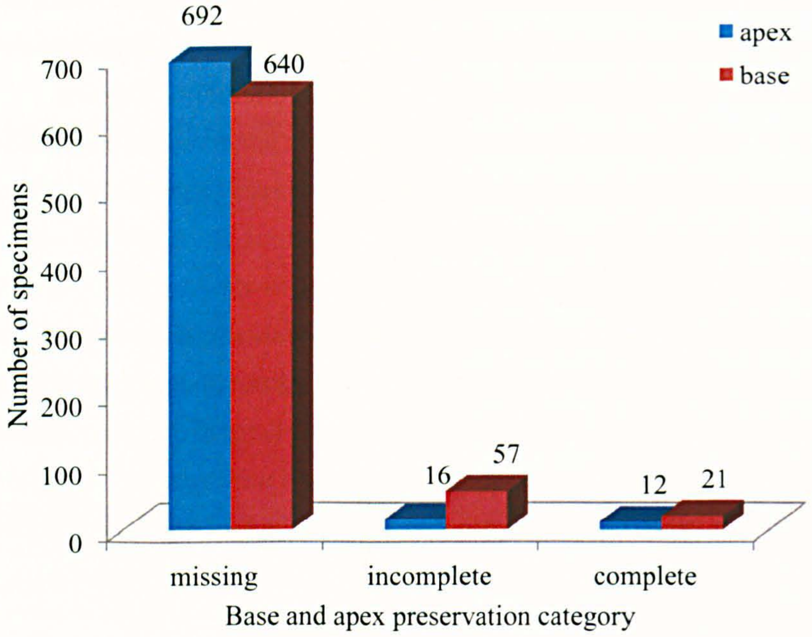

Figure 3.8. Apex and base preservation of the angiosperm leaf specimens of Allt Mor, showing the number of specimens with missing, incomplete and complete apexes or bases.

Apex and base preservation for the Allt Mor specimens is poor as 692 (96%) and 640 (89%) of the specimens do not have apexes or bases preserved (Figure 3.8). Overall apex preservation is more limited with only 4% of specimens with either incomplete or complete apex preservation, while 11% of specimens have incomplete or complete base preservation. Ten specimens in the Allt Mor collection have both an apex and base preserved, which indicates that preservation of both structures on the leaves of Allt Mor is limited. This indicates that the use of apexes and bases for taxonomic or palaeoclimate interpretations may be reduced.

3.5.5 Specimen preservation quality

To assess the quality of preservation for each of the Allt Mor leaf specimens their degree of fragmentation, clarity of venation, margin preservation, apex and base preservation were considered. Each specimen was scored for its preservation quality based on these features; the scores given for each feature are presented in Table 3.5, which was adopted from Hayes (1999). The combined score for each leaf specimen was then used to determine its quality by giving it a rating that ranges very poor to excellent (Table 3.6), i.e. a leaf specimen with a score 6 has a "fair" rating. The overall leaf rating for the Allt Mor collection is summarized in Figure 3.9.

Table 3.5. Scores for fossil leaf characters and features used to determine leaf specimen quality.

Leaf character or feature	Scoring	Leaf character or feature	Scoring
Degree of fragmentation	Almost complete = 3 Fragment =2 Small fragment = 1	Apex	Complete = 2 Incomplete = 1 Missing = 0
Clarity of venation	Very clear = 5 Clear = 4 Fairly clear = 3 Fairly unclear = 2 Unclear =1	Base	Complete = 2 Incomplete = 1 Missing = 0
Margin	Clear = 2 Small percentage = 1 Absent = 0	Both apex and base present	Yes = 1 No = 0

Table 3.6. Preservation rating of fossil angiosperm leaves.

Preservation Rating	Score
Excellent	>12
Very Good	11--12
Good	9--10
Fairly Good	7--8
Fair	5--6
Fairly Poor	4
Poor	3
Very Poor	2

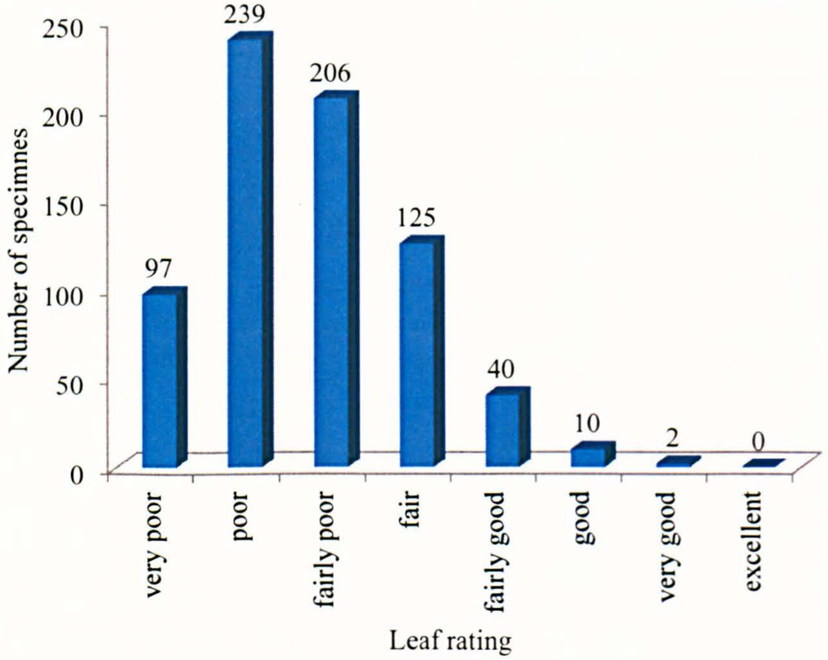

Figure 3.9. Leaf rating of the Allt Mor fossil angiosperm specimens, showing the number of specimens in each category.

The fossil angiosperm leaf rating ranges from very poor to very good, with poor (239 specimens), fairly poor (206 specimens) and fair (125 specimens) being the most common leaf ratings (Figure 3.8). Leaves with very poor to fairly poor rating account for 75% of the specimens, while leaves with fair to very good ratings account for 25% of the specimens. This indicates that the overall preservation of the angiosperm leaves of Allt Mor is relatively poor, but some of the specimens are relatively well preserved.

3.5.6 Estimates of leaf size and length:width ratios

Determining the original size of the fossil leaves of Skye is important because leaf size is used for palaeoclimate analysis, particularly precipitation estimates (Wolfe 1993, Wing and Greenwood 1993, Burham 1997, Wilf 1997, Wiemann et al. 1998). Length:width ratios are also an important aspect of palaeoclimate analysis and therefore must be determined. Leaf size was determined digitally by using ImageJ software (Abramoff et al. 2004). Digital photographs and line drawings of the fossil specimens were imported into ImageJ to measure each leaf specimen's laminar area. The perimeter of each leaf fragment was traced in ImageJ using the polygon selection tool which enables accurate area measurements to be calculated more rapidly. This method was compared with free hand tracing of the perimeter and was shown to be comparable, which indicated that the polygon selection tool was an accurate method for determining laminar area.

The area estimate obtained from the tracing the perimeter of the leaf specimen can then be used to determine the original laminar size class used in leaf morphotyping and climate analysis (e.g. Wolfe 1993, Kovach and Spicer 1995, Wing and Greenwood 1993, Ellis et al 2009). The perimeter of more fragmented specimens are less likely to provide accurate estimates of the original size class of the leaf. To account for this, estimates of the original laminar were made by using the curvature of the leaf margin and the leaves symmetry to determine its original area.

Measurements of each specimen's laminar area were taken, for use in climate analysis, and to determine the range of sizes in the Allt Mor collection. Leaf size classes were determined by Webb (1959), which is regarded as a standard in palaeobotany (Wolfe 1993, Kovach and Spicer 1995, Ellis et al. 2009) (Table 3.7). The distribution of leaf sizes for the Allt Mor collection is summarized in Figure 3.10.

Table 3.7. Leaf size classes from Webb (1959).

Leaf size Class	Laminar area (mm^2)	Leaf size Class	Laminar area (mm^2)
leptophyll	<25	Mesophyll	4500-18225
Nanophyll	25-225	Macrophyll	18225-164025
Microphyll	225-2025	Megaphyll	>164025
Notophyll	2025-4500		

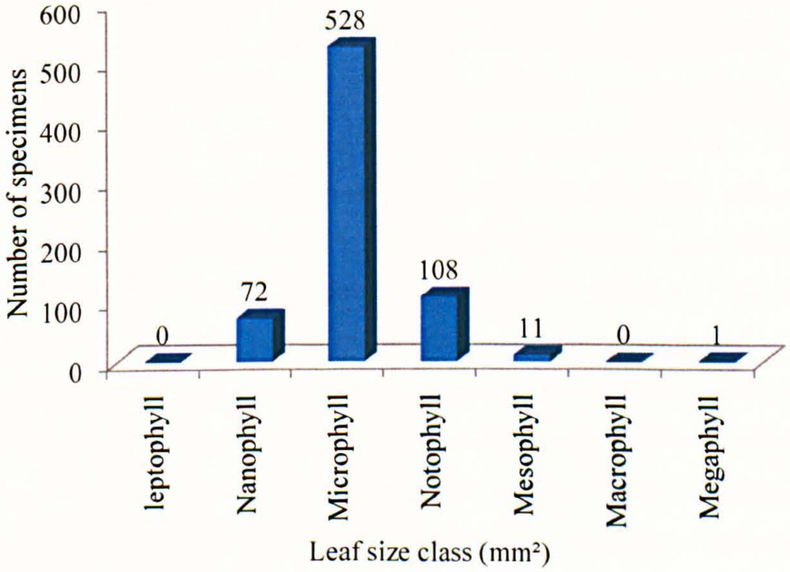

Figure 3.10. Leaf size class distribution for the fossil angiosperm leaves of Allt Mor.

The most abundant size class in the Allt Mor collection is microphyll, which accounts for 528 (73%) of the specimens measured. Nanophyll and notophyll size classes are the next most abundant and account for 72 (10%) and 108 (15%) of specimens respectively. This distribution is largely a reflection of the degree of leaf fragmentation rather than the original size distribution of the leaves, as such a high percentage of the leaves (96%) are small fragments. It is likely therefore that Allt Mor flora was dominated by plants that had microphyll to mesophyll leaf size classes.

Determining the length:width ratio of the leaves is only reliable if the leaf is nearly complete. Since less than 1% of the collection was considered nearly complete it was decided that calculating the L:W ratios for the whole collection would provide an inaccurate representation of the flora. Individual ratios were calculated for some leaves that were more fragmented if their original lengths or widths on one side of the laminar were preserved. To determine the length:width ratio the leaf specimen's length and width were measured in ImageJ and the ratio was then calculated from these measurements.

3.5.7 Summary

The subsample of 720 leaves used to assess the preservation of the Allt Mor angiosperms indicates that the leaf specimens are highly fragmented, with poor to fair venation clarity and predominately lack marginal, apex or basal preservation. Leaf ratings based on these characters and features indicated that the most common ratings of the angiosperm leaves were poor to fair. Measurements of laminar size indicate the leaf fragments of Allt Mor are predominately microphyll with notophyllous and nanophyllous specimens being the next most common.

3.6 The morphotype concept

The classification of modern angiosperms is based on their reproductive structures (Takhtajan 1980, Ash et al. 1999), this is also applies to fossil plant taxa. For fossilized leaves to be accurately identified they must be attached to reproductive structures. Leaves attached to reproductive structures are, however, relatively rare, and disarticulated leaves are more common in fossil plant assemblages (Ash et al. 1999). It is common procedure, therefore, to divide the leaves into morphotypes by identifying morphological characters that are systematically useful. A morphotype is an informal taxonomic category that is independent of the Linnaean nomenclature system, the leaf morphotypes are equivalents to biological species, but should not be considered to be precise species equivalents (Ash et al. 1999).

Disarticulated fossil leaves dominate the plant assemblages of Skye, attached reproductive structures are absent, and seeds and fruits are too poorly preserved to be of systematic value. The angiosperm leaves from Skye were organised into morphotypes to classify them.

3.6.1 Visual and categorical grouping of leaves

Angiosperm leaf morphology can be readily categorized into three broad aspects: laminar form, venation and margin. Several authors (Dilcher 1974, Hickey and Taylor 1991, Ash et al. 1999, Candela et al. 1999, Ellis et al. 2009) have used morphological characters of angiosperm leaves in an attempt to better characterize them and use these features to determine taxonomic relationships. Ellis et al. (2009) have produced a manual of leaf architecture, which describes aspects of angiosperm leaf morphology in great detail. This manual has proven exceptionally useful for identifying and describing the morphology of the Skye angiosperm leaves.

3.6.2 Leaf morphological bins

Leaf bins represent broad morphological groups that share several characteristics in common. The Palaeobotany Project founded by the Denver Museum of Nature and Science (www.paleobotanyproject.org) has outlined the procedure of binning fossil floras. The flow chart (Figure 3.11) demonstrates the stages of binning flora. The initial phase involves separating the dicotyledonous angiosperms from angiosperm plant remains and other plant groups such as conifers and ferns. Woody dicots can be readily identified by their board leaf shape and net-like structure of their veins.

Later stages of binning involve sorting the leaf collection by the morphological characters (Figure 3.11). Ideally all specimens should have all necessary characters preserved to be sorted into final leaf bins, but this is rarely the case. Leaves that are too poorly preserved to be categorized are placed into a separate unsortable bin and these specimens may still be recognisable. The binning process is a useful tool to quickly differentiate leaf types. The fossil specimens within the bins may represent different fossil taxa. A more detailed morphological approach is therefore required to differentiate the fossil specimens into separate morphotypes.

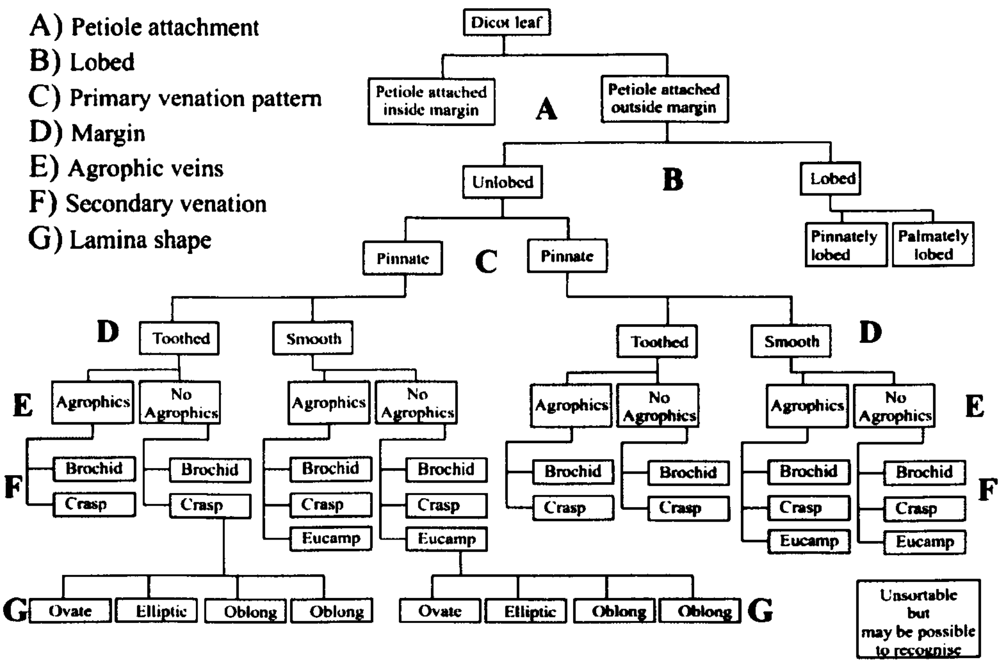

Figure 3.11. Tree diagram used for binning fossil angiosperm leaves for morphotype recognition. Each box represents a morphological bin. Redrawn from the paleobotany project (www.paleobotanyproject.org).

3.6.3 Differentiating morphotypes

The best preserved specimens from the final bins and some leaves from the unsortable bin were selected to obtain a more detailed morphological profile of the leaf specimens. The leaf architectural manual (Ellis et al. 2009) was used to describe the morphology of the leaf specimens.

Comparisons were also made with the fossil angiosperm leaves of Ardtun, Mull (Boulter and Kvacek 1989). This was done for three reasons: 1) the Ardtun leaf assemblage from Mull is from the same region as Skye (BTVP) and it is of a similar age (see Chapter 2, section 2.3), 2) initial comparisons of the floras of Skye and Ardtun, Mull indicate that they appear to share many of the same plant taxa, 3) fossil leaves from Ardtun are often exceptionally well preserved and often complete. The leaves from Ardtun were therefore used as a guide to help describe the morphology of the more fragmented angiosperm leaves of Skye.

3.7 Angiosperm morphotypes of Skye

In total 14 woody dicotyledonous angiosperm morphotypes have been identified in the leaf assemblages of Skye. Sections 3.8 to 3.16 contain detailed information of each morphotype including the specimen numbers attributed to the morphotype, a diagnosis of its morphology, an identification to known fossil plant taxa (where possible), a discussion on the morphology and variability of each morphotype, and comparisons with possible fossil and modern relatives.

3.8 Angiosperm morphotype 1 (AM1)

3.8.1 Specimens

The specimen numbers of this morphotype are: ACC: 001-c, 015, 016-a, AM.NA: 0001-c, 0001-h, 0002-c, 0004-c, 0008, 0018-c, 0049-a, 0049-c, 0058, 0062-b, 0076, 0077-e, 0078-b, 0080-c, 0096, 0111-a, 0112, 0113, 0125-a, 0125-b, 0125-c, 0126-c, 0130, 0136-a, 0144-a, 0147-a, 0160-a, 0169-b, 0174-c, 0175-b, 0176-a, 0176-b, 0179-a, 0179-b, 0179-c, 0186-a, 0187-a, 0196, 0199, 0200-c, 0201, 0205, 0207-b, 0207-c, 0211-b, 0217, AM.NA.2008: 001-b, 008-c, 003-b, 005, AM.NA.2008: 020-a, 022-a, 022-d, 022-e, 024, 035-a, 035-c, NMS.G.2004.29: 015-d, 028-b, 051-d, 052, 063-a, 066-h, NMS.G.2006.5.1-a, ACC.AM.031-b.

3.8.2 Diagnosis

Leaf attachment petiolate. Blade attachment marginal, laminar size microphyll to macrophyll, laminar L:W ratio unclear, laminar shape obovate or elliptic, blade medially symmetric or asymmetric, base symmetrical, lobed, margin serrate. Apex nor preserved, base angle acute or obtuse, base shape concave-decurrent, concavo-convex or rounded. Primary venation palinactinodromous, naked basal veins absent, one, three or five basal veins, simple agrophic veins. Major secondary veins craspedodromous, interior secondary veins present, minor secondary course appears craspedodromous, major secondary vein spacing irregular, secondary vein angle irregular to increasing proximally, major secondary vein attachment proximally decurrent. Intersecondary span less than 50% of subjacent secondary, occur less than or more than one per intercostals area, proximal course parallel to major secondary, and distal course perpendicular to subjacent major secondary Intercostal tertiary veins mixed percurrent with obtuse vein angle that decrease exmedially. Epimedial tertiary veins opposite percurrent with proximal course acute to midvein and distal course parallel to intercostals tertiary. Quaternary vein fabric mixed percurrent. Quinternary vein fabric present but unclear, areolation development good, marginal ultimate venation unknown. Tooth morphology unclear.

3.8.3 Identification

Leaves of angiosperm morphotype 1 (AM1) are mostly highly fragmented and none are complete. Venation characteristics are, however, often well preserved, which enables a more reliable identification of this morphotype. AM1 shows significant similarities to *Platanites hebridicus* of Ardtun, Mull (Crane et al. 1988, Boulter and Kvacek 1989). AM1 and *Platanites hebridicus* share the same venation pattern; both leaf types have palinactinodromous primary venation with three major primaries and craspendodromous major and minor secondary venation. *Platanites hebridicus* has secondary vein angles that are between 45 ° to 60 ° (Crane et al. 1988), which falls within the same range of the Allt Mor leaves (48 ° to 59 °).

Both leaf types have pronounced interior secondary veins, which form distinctive arches. Intersecondary morphology is similar, as both leaf types either have several in each intercostals area or lack them entirely. When the intersecondary veins are present they have a relatively short course before they join the intercostal tertiary veins. Tertiary venation is similar for both AM1 and *Platanites hebridicus*. Both have mixed percurrent intercostal veins, and opposite percurrent epimedials with an acute course relative to the midvein and a distal course that is parallel to the intercostal tertiary veins. Higher order venation is similar with mixed percurrent quaternary veins. One apparent difference in vein morphology between the Skye and Mull leaf types is that some of the Skye leaves have very pronounced thick veins, which are less pronounced in the Mull leaves. This may be due to differing preservation conditions between the localities or may be related to the larger size of the Skye forms, which, as result of their larger laminar, areas had thicker veins.

Both leaf types have concavo-convex or decurrent base shapes, where in the latter case the basal margin extends along the petiole, although this characteristic is more pronounced in the Skye leaves. Another similarity between the two leaf types is the presence of a long thick petiole. *Platanites hebridicus* leaves of Ardtun have two smaller leaflets present at or near the base of this petiole, which indicates the leaflet arrangement was trifoliate (Crane et al. 1988). The terminal leaflet is larger, lobed with palinactinodromous primary venation, which is similar to the Skye specimens. The two smaller leaflets are pinnate and unlobed, but their secondary, tertiary and quaternary venation is broadly similar to the larger terminal leaflet. Lateral leaflets of AM1 leaves have not been recognized from the Allt Mor assemblage, which may be a taphonomic anomaly due to the high degree of fragmentation associated with this morphotype.

The similarities in venation patterns and basal morphology between AM1 and *Platanites hebridicus* are strong. This indicates that the two leaf types may represent the same plant taxon. The lack of lateral leaflets of the Skye form to some extent limits the comparison between the two leaf types, but this may be related to the poor preservation of the Skye forms rather than a true morphological difference. It is therefore likely that these two leaf types represent the same plant taxon, and AM1 is considered as *Platanites hebridicus.*

3.8.4 Discussion

This morphotype shows significant variability in overall form and size. Leaf size classes range from microphyll to macrophyll (1693- 48064 mm^2). Due to the high degree of fragmentation of the specimens it is difficult to determine their original size. Even though some of the specimens are highly fragmented it is clear that some were originally in the mesophyll size class, or possibly greater prior to fragmentation (e.g ACC.012, AM.NA.008, NMS.G.2006.5.1-a) (Figure 3.12). Not all of the specimens of this morphotype are large, however, as two smaller specimens (AM.NA.002-c and 0077-e) are microphyllous (Figure 3.13). These smaller leaves may represent immature foliage that was dislodged from the source vegetation prior to its complete development, or they may represent smaller sun leaves from the canopy. The more common, larger leaves of this morphotype may represent shade or sucker foliage that developed in lower light conditions.

Laminar shape is unclear but based on the widest part of the laminar preserved the leaves appear to be either elliptic or obovate. Laminar shape in AM1 appears to be influenced by the angle of the outer primary veins. Leaves with more obtuse primary vein angles tend to be more obovate (e.g. ACC.001-c), while those with more acute angled primaries appear to be elliptic (e.g. AM.NA.2009.020-a, AM.NA.002, AM.NA.077-e, AM.NA.199-a) (Figure 3.12, Figure 3.13). Determining if the leaves of AM1 were lobed is difficult to determine due to fragmentation of the specimens, but one specimen, AM.NA.002 appears to have a sinus between the midvein and outer primary, indicating that it may be lobed (Figure 3.12). A reconstruction of *Platanites hebridicus* leaf in Crane et al. (1988) indicates that the Ardtun forms were indeed lobed, although relatively weakly. This indicates that *Platanites* leaves of Skye may have also been lobed.

Base angle is variable. It can be acute (~68 °) (e.g. AM.NA.002, AM.NA.077-e), while one specimen ACC.001-c appears to have an obtuse base with an angle of ~135°. Base shape is equally variable and several of the microphyllous specimens have concave-decurrent base shapes (e.g. AM.NA.002, AM.NA.077-e) with laminar tissue extending along the petiole (Figure 3.12). This morphology is associated with leaves that have more acute outer primary veins relative to the midvein. Specimens with more obtuse outer primary veins appear to have a concavo-convex base shape (e.g. ACC.001-c).

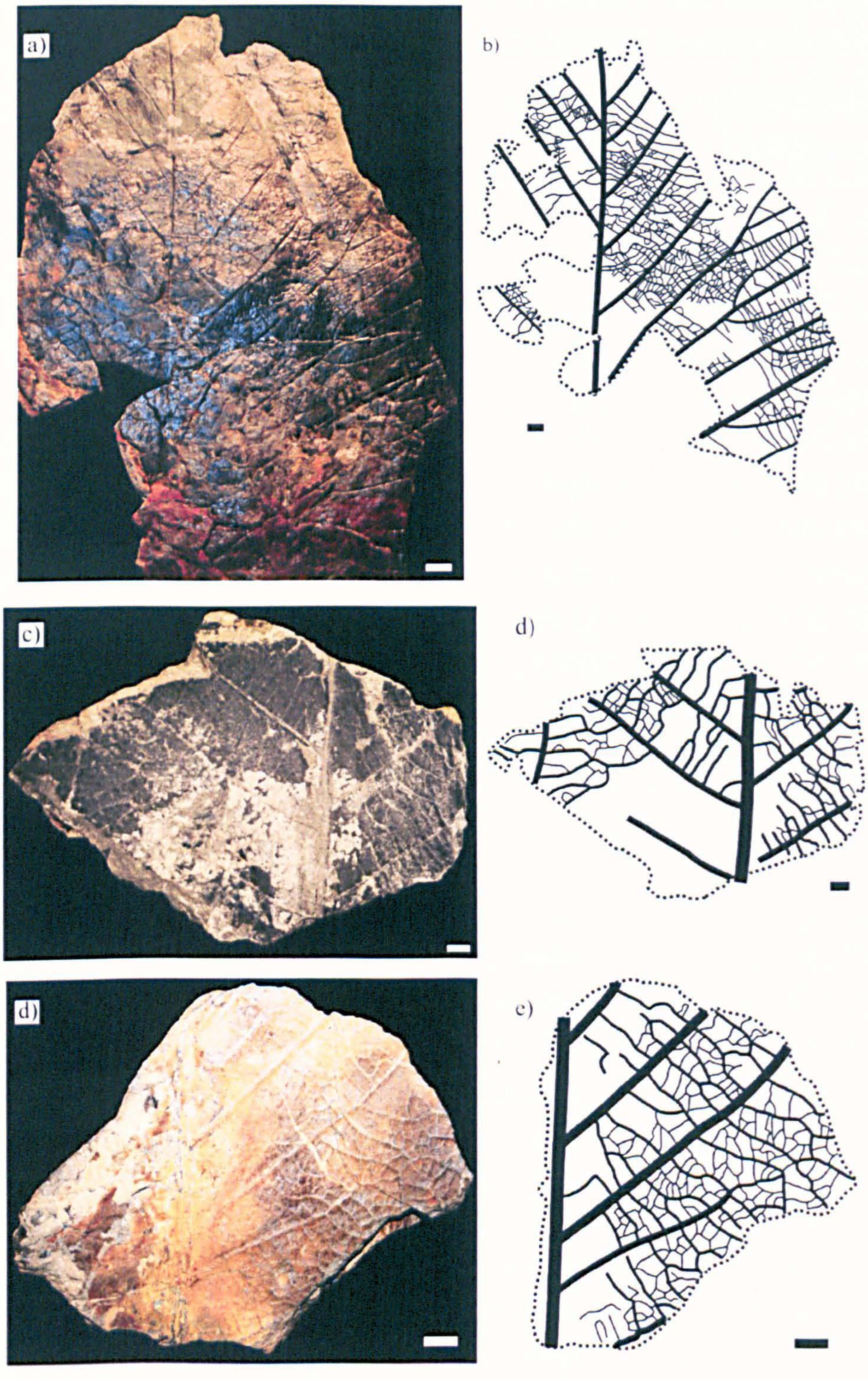

Figure 3.12. Large but fragmented specimens of AM1 a) NMS.G.2006.5.1-a, b) line drawing of NMS.G.2006.5.1-a, c) ACC.012, d) line drawing of ACC.012, d) AM.NA.008, e) line drawing of AM.NA.008. Scale bars = 1 cm.

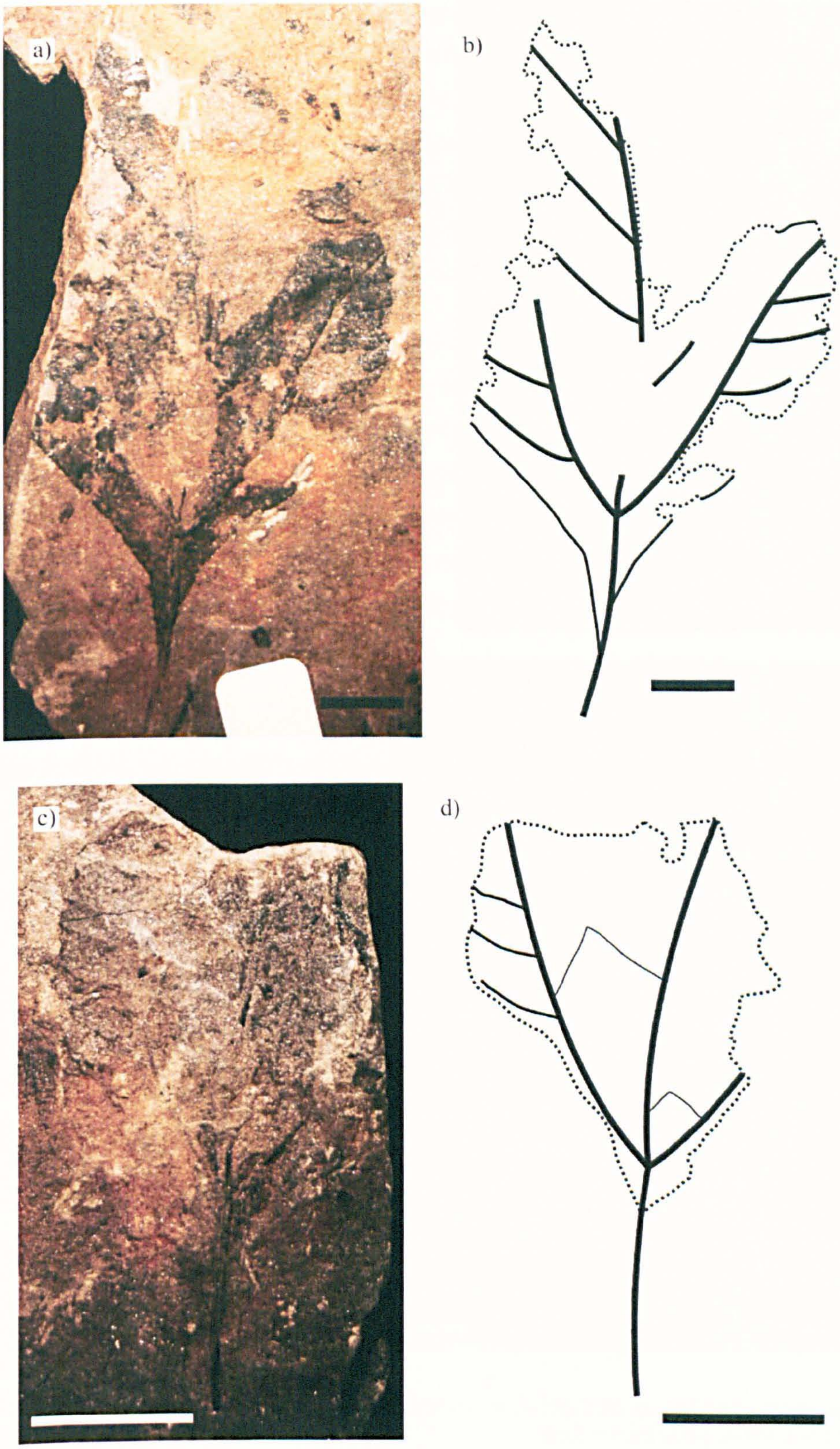

Figure 3.13. Microphyll specimens of AM1. a) AM.NA.002-c, b) line drawing of AM.NA.002-c, c) AM.NA.077-e, d) line drawing of AM.NA.077-e. Scale bars = 1 cm.

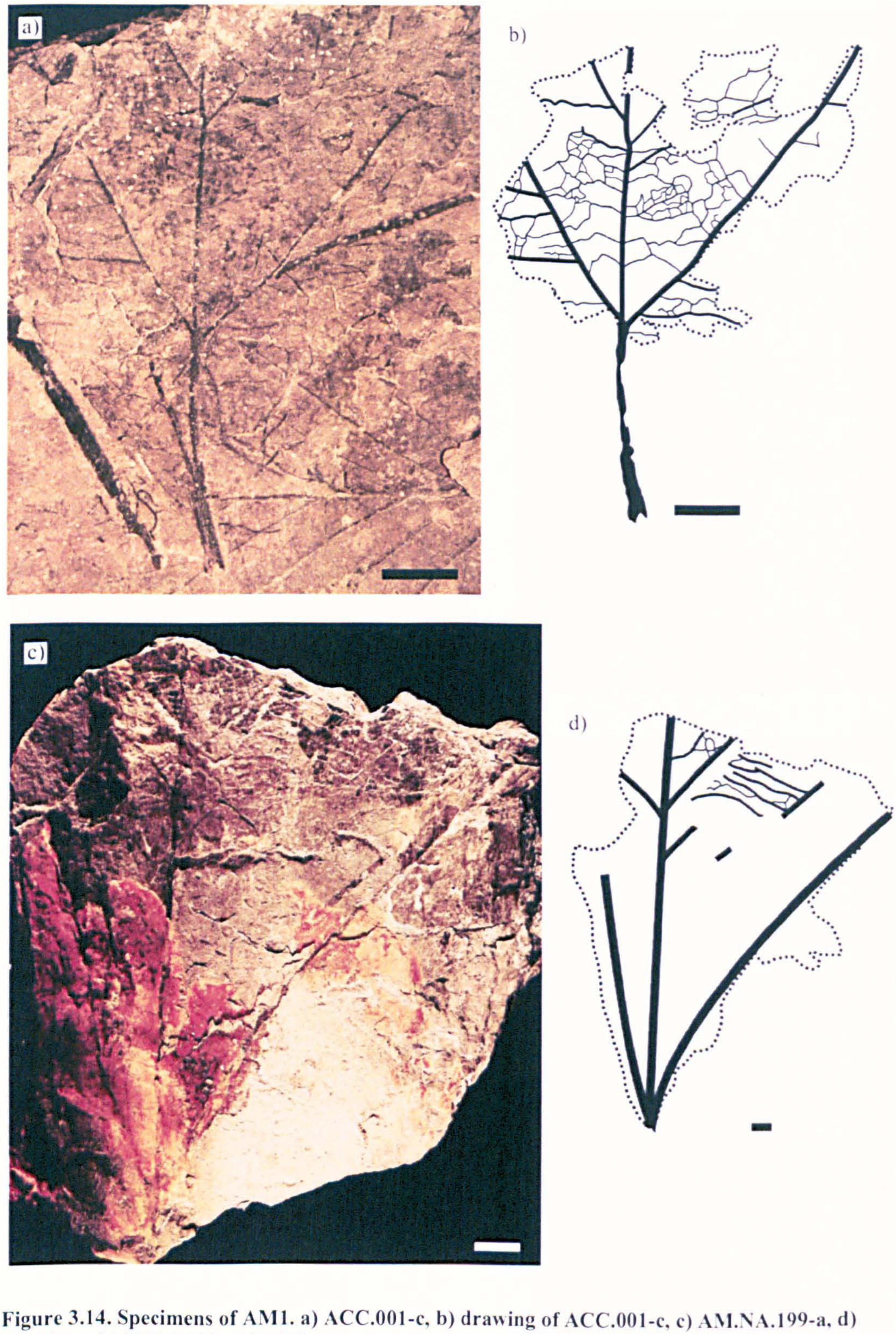

Figure 3.14. Specimens of AM1. a) ACC.001-c, b) drawing of ACC.001-c, c) AM.NA.199-a, d) drawing of AM.NA.199-a. Scale bars = 1 cm.

Venation patterns in this morphotype are highly distinctive, which has facilitated the identification of even highly fragmented specimens. The tertiary, quaternary and quinternary veins appear to have formed an impression in the sediments before they were consolidated. These impressions have been preserved and have led to an almost scale-like appearance (e.g. NMS.G.2006.5.1-a, AM.NA.008, AM.NA.199-a, AM.NA.179-b) (Figures 3.12 to 3.15). This feature appears to be restricted to the larger specimens, whose veins would have been thicker and therefore created a more pronounced mold or cast into the sediment.

Interior veins, when preserved, are typically present in the upper portion of the laminar (e.g. AM.NA.179-b) where they form distinctive arches that curve towards the distal margin (Figure 3.15). Spacing of the secondary veins is highly variable within the same specimen indicating an irregular spacing pattern. Secondary vein angle variability is equally inconsistent; vein angles typically range from 35 ° to54 ° in the central portion of the laminar, and 48 ° to 59 ° in the proximal section of the laminar. Intercostal tertiary veins are obtuse to the midvein; admedially they range from 107 ° to 141 ° and exmedially range from 109° to 122°, indicating that intercostals vein angle decreases exmedially.

Tooth morphology is unclear as the margin is rarely preserved but some specimens do appear to have teeth but they are poorly preserved (e.g. AM.NA.2009.020-a, AM.NA.002-c) (Figures 3.13-a and 3.15-a). Tooth shape is unclear but it appears that their shape may be concave on the distal flank and convex on the proximal flank. Ardtun specimens of *Platanites hebridicus* have well preserved margins, which indicate that the leaves of AM1 were toothed.

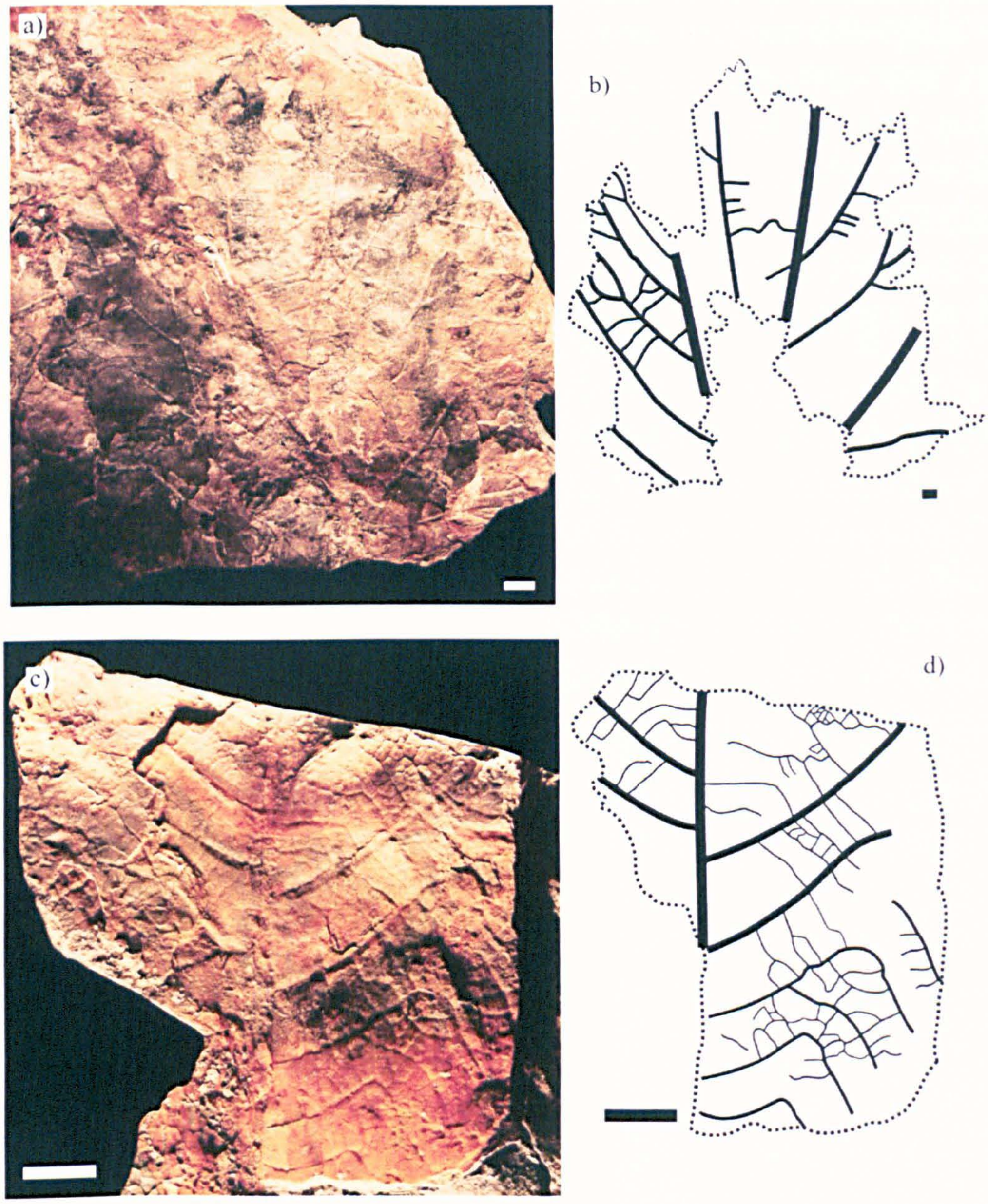

Figure 3.15. Specimens of AM1. a) AM.NA.2009.020-a, b) line drawing of AM.NA.2009.020-a, c) AM.NA.179-b, line drawing of AM.NA.179-b. Scale bars = 1 cm.

3.8.5 Similarities to other fossil taxa

Fossil representatives of the Platanaceae are common elements of Northern Hemisphere floras of the Late Cretaceous and Paleogene (Crane et al. 1988, Pigg and Stockey 1991, Manchester 1999, Kvacek et al. 2001, Kvacek and Manchester 2004, Golovneva 2007, Tschan et al. 2008). Several leaf types have been recognized, which vary significantly in their overall form (Boulter and Kvacek 1989). AM1, as discussed in section 3.8.3 is attributed to the form genus *Platanites*. This Paleocene representative of the Platanaceae with its distinctive trifoliate foliage has only been documented in Alberta and Scotland of Paleocene age (Crane et al. 1988, McIver and Basinger 1993, Boulter and Kvacek 1989, Manchester 1999).

Platanites leaves have been recovered from the Early Paleocene Ravenscrag Formation of Saskatchewan, Canada (McIver and Basinger 1993). *Platanites sp.* of the Ravenscrag Formation shares many similarities with *Platanites hebridicus* with its distinctive trifoliate leaf arrangement, larger palinactinodromous terminal leaflet and smaller pinnate lateral leaflets. Both forms also share the same overall venation pattern (Crane et al. 1988, McIver and Basinger 1993, Boulter and Kvacek 1989). The base shape is similar with a marginal extension along the petiole which is more pronounced than *Platanites hebridicus* of Ardtun, and resembles the base shape of the smaller specimens from Allt Mor (Crane et al. 1988, McIver and Basinger 1993). The terminal leaflets of the Canadian *Platanites* do, however, differ from the Scottish forms. The margin of *Platanites* sp. has considerably more teeth and appears unlobed (Crane et al. 1988, McIver and Basinger 1993). The lateral leaflets are also smaller and more elongate compared to lateral leaflets of the Ardtun specimens (Crane 1988, McIver and Basinger 1993).

The absence of this leaf type in other mid to high latitude plant-bearing sites is unusual, but this distribution indicates that plant species were able to migrate from North America into Scotland during the Paleocene. The Early Paleocene Canadian representative of *Platanites* is older (~64 Ma) than mid Paleocene forms in Scotland, which may indicate that *Platanites* may have originated in North America and migrated into Scotland via the Arctic during the Early Paleocene.

3.8.6 Similarities to modern taxa

Fossil leaves of *Platanites hebridicus* share many characteristics with modern *Platanus* foliage (Crane et al. 1988). The characteristic palinactinodromous primary venation, craspendromous secondary veins, higher order venation, and leaf polymorphism of modern Platanaceae is nearly identical to that of *Platanites hebridicus* (Crane et al. 1988). Modern *Platanus* leaves do, however, lack lateral leaflets, which are a characteristic feature of *Platanites* (Crane et al. 1988, McIver and Basinger 1993). Crane et al. (1989) described fossil Platanaceae-like reproductive structures from Ardtun, Mull, which are tentatively associated with *Platanites* foliage. The fossil staminate flowers and fruiting heads share many characteristics with modern *Platanus*, but differ in several key morphological characters (Crane et al. 1989). The dissimilarities of the fossil and modern reproductive structures indicate that the reproductive morphology of modern planes was not fully established in the Paleocene. The relatively fragmentary remains of *P. hebridicus* from Skye makes assigning of this morphotype to a modern taxon problematic. The close similarity of AM1 with the well preserved leaves from Mull and Canada, and their similarities to modern planes, indicates that AM1 represents an extinct form of the Platanaceae.

3.9. Angiosperm morphotype 2 (AM2)

3.9.1 Specimens

The specimen numbers of this morphotype are: AM.NA: 007-b, 014-a, 014-c, 014-d, 016-b, 040-a, 059-b, 082-c, 082-i, 084-f, 084-i, 084-m, 097-a, 124-a, 138-a, AM.NA.2008: 005-a, 006-e, 006-f , AM.NA.2008: 018-b, NMS.G.2004.29: 026-c, 004-b, 005-a, 023-g, 023-h, 031-d, 034-c, 047-b, 055-i, 061-a, 072-c, 072-d, 079-a, 079-b, 079-c, 079-g, 081-d, NMS.G.2002.64: 3-b, 3-e, 5-f, 5-I.

3.9.2. Diagnosis

Blade attachment marginal, laminar size ranging from microphyll to mesophyll, laminar length:width ratio varying from ~1:1 to ~1.4:1, laminar shape ovate or elliptic, blade medial symmetry symmetrical to slightly asymmetrical. Margin is unlobed and serrate with an obtuse apex angle, shape unclear either convex or acuminate without a drip tip, reflex base angle, and cordate base shape. Primary venation is basal actinodromous with no naked basal veins, seven to nine to seven basal veins, and simple agrophics veins. Major secondaries simple semicraspedodromous with spacing that is irregular or increases abruptly proximally, inconsistent angles, and excurrent or deflected attachment to the midvein. Interior secondaries present, minor secondaries semicraspedodromous. Intersecondary veins absent. Intercostal tertiary veins mixed percurrent. Epimeidal tertiary veins mixed percurrent with a proximal course parallel to intercostal tertiaries and distal course acute to the midvein. Exterior tertiaries appear looped. Quaternary vein fabric mixed percurrent to irregular reticulate. Aerolation shows moderate to good development. Freely ending veinlets appear absent, marginal ultimate venation looped. Tooth spacing regular with one order of teeth and 2-3 teeth/cm. Sinus shape angular to rounded and tooth shape convex/convex or concave/convex. Principal vein present and terminates either at the tooth apex or the distal flank. Accessory vein course looped. Tooth apex appears simple.

3.9.3 Identification

Angiosperm morphotype 2 (AM2) is represented by many relatively well preserved leaf specimens. Its overall form, including margin, apex and base are present in some specimens and its venation clarity, is often clear. Due to this morphotype's higher degree of preservation it is possible to identify it to a known fossil taxon. The overall leaf form of this of AM2 indicates that it is similar to *Trochodendroides antiqua* of Ardtun, Mull (Boulter and Kvacek 1989). Both leaf types have the same elliptic laminar shape, cordate base and serrate margin with rounded tooth apexes. The venation patterns are identical at all orders providing further evidence that AM2 is the same taxon as *Trochodendroides antiqua* from Ardtun. AM2 and *Trochodendroides antiqua* have well defined teeth with convex distal and proximal flanks, or less frequently convex distal flanks. Specimens from Ardtun often have elongated teeth that appear as finger-like projections from the margin. This character is less well developed in the Allt Mor specimens but may be related to limited preservation of the margin at this locality. Based on the strong morphological similarities between AM2 and *Trochodendroides antiqua* they are regarded as the same species.

3.9.4 Discussion

The morphology of AM2, as mentioned in 3.9.3, is well understood because of several well preserved specimens (e.g. NMS.G.2004.29.047-b, NMS.G.2004.29.079-a, NMS.G.2004.29.072-c, NMS.G.2004.29.023-g, NMS.G.2002.64.5-f, AM.NA.082-c) (Figures 3.16, 3.17). Laminar size is variable and specimens range from microphyll (1031 mm^2) to mesophyll (6505 mm^2) (estimated original laminar area), but the majority are within the upper range of microphyll to lower range of notophyll. The preservation of this morphotype has enabled length to width ratios to be estimated. Laminar length:width ratio are typically ~1:1 (e.g. NMS.G.2004.29.047-b, NMS.G.2004.29.072-c, NMS.G.2004.29.079-a) (Figures 3.16-a, c, e) but can be greater with ratios of ~1.8:1 to 2:1 (e.g. NMS.G.2002.64.5-i, AM.NA.082-c) (Figures 3.17-e, 3.18-e).

The apexes of AM2 have been partially preserved in at least three specimens (AM.NA.082-c, NMS.G.2002.64.3-e, NMS.G.2002.64.5-f) (Figure 3.17-c, e). Specimens AM.NA.082-c and NMS.G.2002.64.5-f apex shape is convex (Figure 3.17-c, e), but specimen NMS.G.2002.64.3-e may have an acuminate apex shape (Figure 3.18-a). The curvature of the margin adjacent to the midvein indicates that it may have terminated below the preserved end of the midvein. This would suggest that the apex may be acuminate and comparisons with better preserved leaves from Ardtun, Mull indicates that some of the leaves have acuminate apexes but they lack the drip tip. This suggests NMS.G.2002.64.3-e may have had an acuminate apex shape that probably lacked a drip tip. Base shape appears to be exclusively cordate, but the depth of the basal sinus varies and it can be relatively shallow (e.g. NMS.G.2004.29.047-b, NMS.G.2004.29.023-h) or deep (e.g. NMS.G.2002.64.5-i) (Figure 3.16-a, 3.18-c, e).

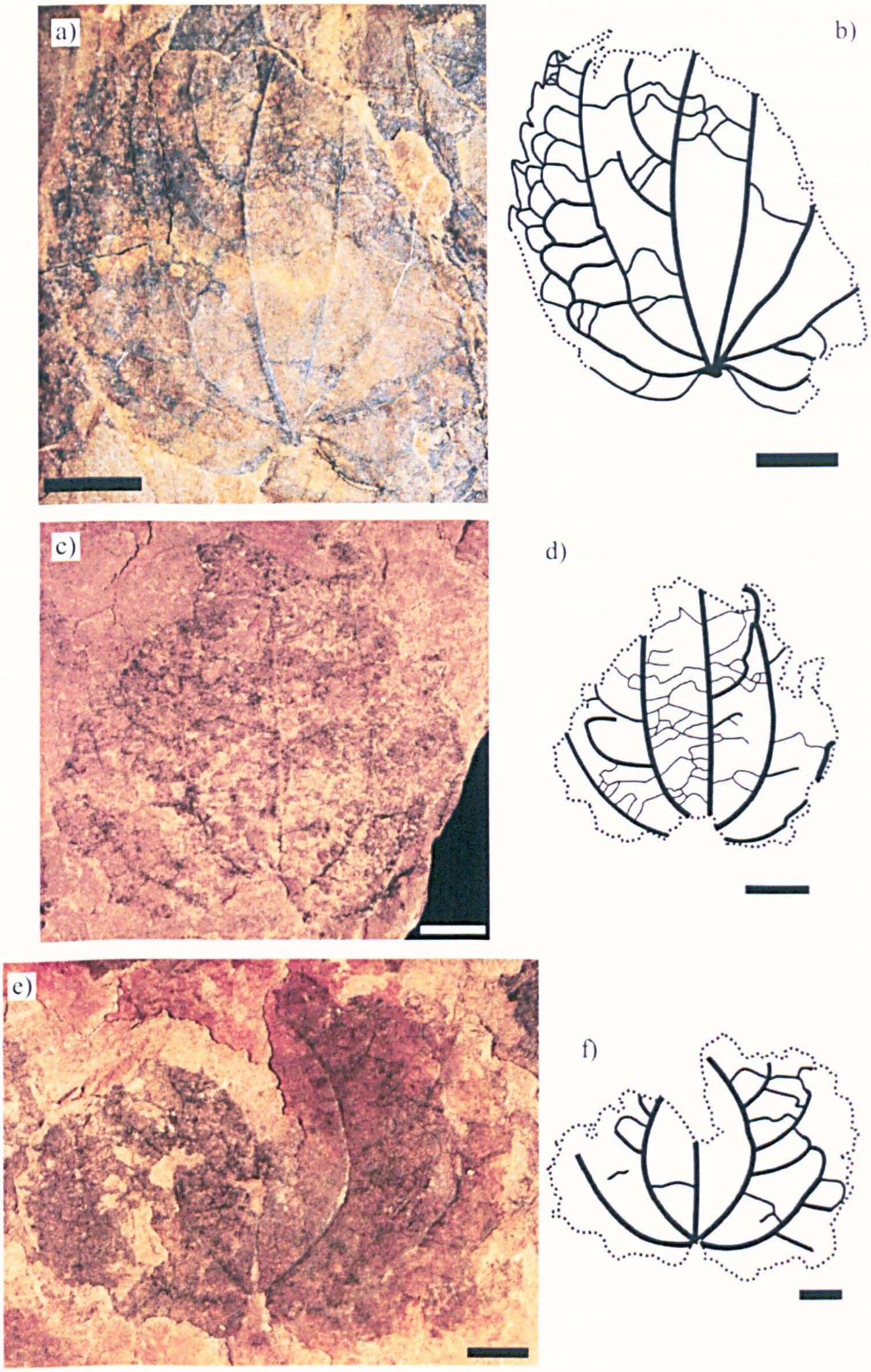

Figure 3.16. Examples of well preserved specimens of AM1. a) NMS.G.2004.29.047-b, b) drawing of NMS.G.2004.29.047-b, c) NMS.G.2004.29.079-a, d) drawing of NMS.G.2004.29.079-a, e) NMS.G.2004.29.072-c, f) drawing of NMS.G.2004.29.072-c. Scale bars = 1 cm.

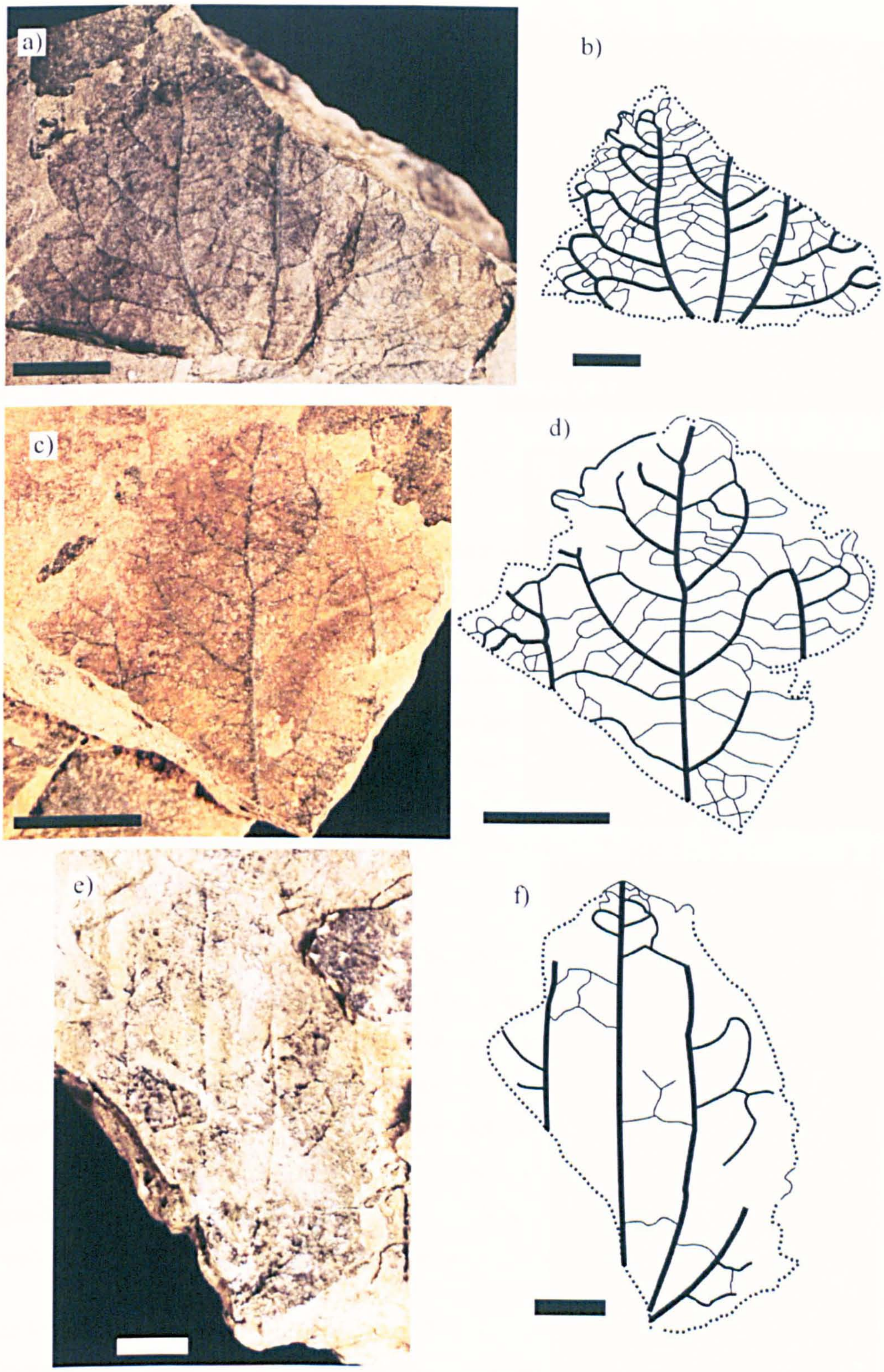

Figure 3.17. Specimens of AM2. a) NMS.G.2004.29.023-g, b) line drawing of NMS.G.2004.29.023-g, c) NMSG.2002.64.5-f, d) line drawing of NMSG.2002.64.5-f, e) AM.NA.82-c, f) line drawing of AM.NA.82-c. Scale bar = 1 cm.

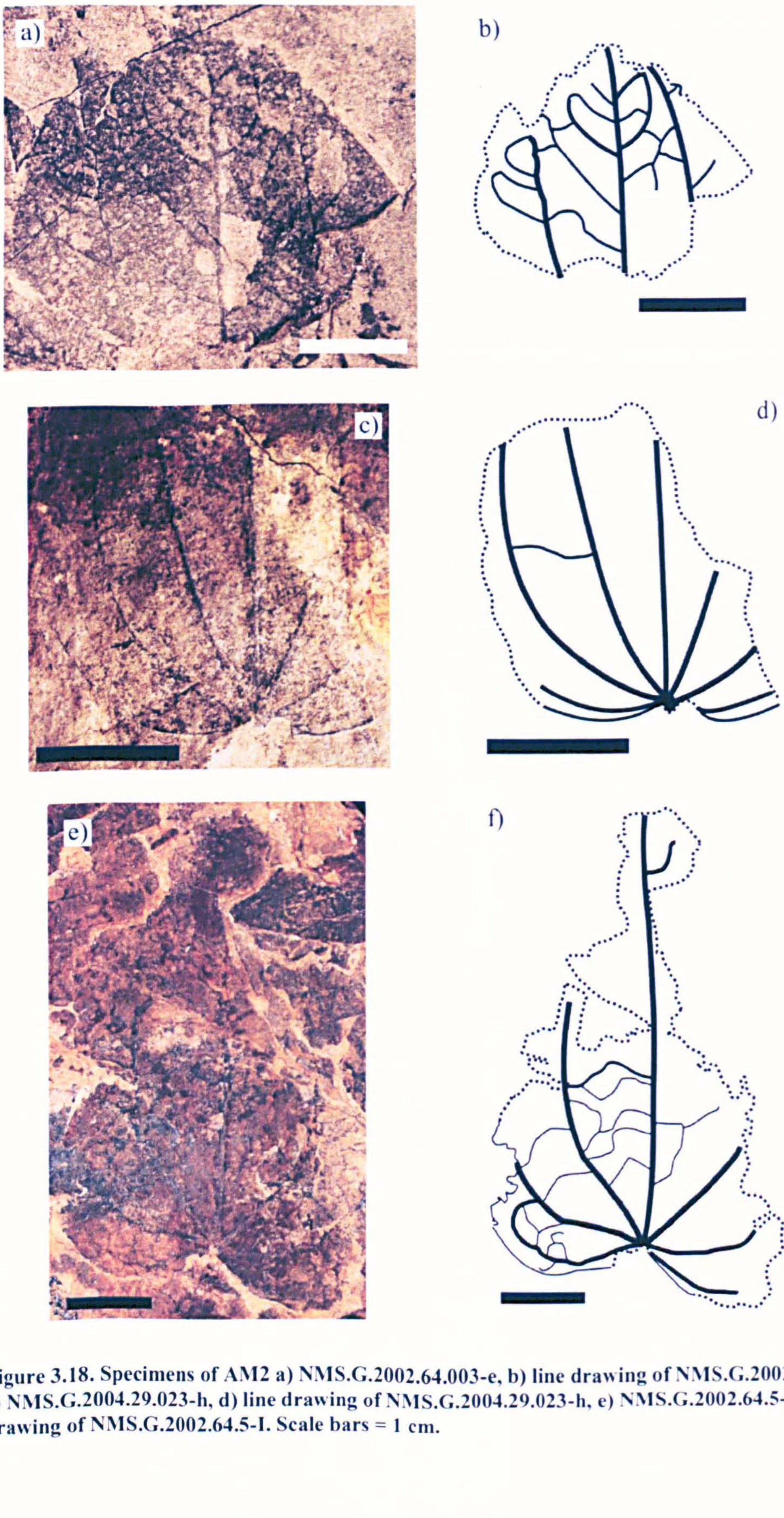

Figure 3.18. Specimens of AM2 a) NMS.G.2002.64.003-e, b) line drawing of NMS.G.2002.64.003-e, c) NMS.G.2004.29.023-h, d) line drawing of NMS.G.2004.29.023-h, e) NMS.G.2002.64.5-I, f) line drawing of NMS.G.2002.64.5-I. Scale bars = 1 cm.

The semicraspedodromous secondary veins are spaced irregularly in this morphotype with spacing ranging from 2mm to 9mm. The variability of the secondary vein angles is irregular; proximal vein angles range from 47 ° to 88 ° (mean 68 °), centrally 40 ° to 83 ° (mean 64 °) and distally 53 ° to 73 ° (mean 59 °). Secondary vein attachment is typically excurrent, although towards the base the secondary attachment can become deflected resulting in a sinuous course to the central primary vein.

Tooth shape is relatively consistent between specimens and the majority of teeth have convex/convex tooth shapes, but in some instances the teeth may have concave proximal flanks. Sinus shape is primarily angular, but where the teeth are more widely spaced the sinus is more rounded.

3.9.5 Similarities to other fossil taxa

The morphology of AM2 indicates that this morphotype is *Trochodendroides antique,* leaves attributed to the form genus *Trochodendroides* were a common element of Late Cretaceous and Paleocene floras of mid to high latitudes of the Northern Hemisphere (e.g. Brown 1939, Koch 1963, Hsu 1983, Crane and Stockey 1985, Kvacek et al. 1994, Herman and Spicer 1996, McIver and Basinger 1999, Falcon-Lang et al. 2004, Craggs 2005, Sun et al. 2007, Akhmetiev and Beniamovski 2009, Herman et al. 2009). A detailed review of this form genus is beyond the scope of this study, but comparisons are made with *Trochodendroides* leaf types found in regions close to the British Tertiary Volcanic Province (BTVP) and a well preserved species in Alberta.

Within the Brito-Arctic region (Scotland, Greenland and Svalbard) leaves associated with *Trochodendroides* and *Cercidiphyllum*-like leaves are abundant (Koch 1963, Boulter and Kvacek 1989, Kvacek et al. 1994). In west and east Greenland *Cercidiphyllum*-like leaves occur throughout the Early Paleocene (pre-volcanic) and Early to mid-Paleocene (inter-basaltic) sequences (Koch 1963). The overall leaf form and venation pattern of the *Cercidiphyllum arcticum* of Greenland is similar to that of *Trochodendroides antiqua* of Mull and Skye. The tooth structure of *C. arcticum* indicates that it is different to the Scottish forms, as its teeth are well rounded, broad, and have poorly developed tooth sinuses.

In Svalbard two Paleogene species have been recognized, *Trochodendroides crenulata* and *T. richardsonii* (Kvacek et al. 1994). These two leaf types are typical of this form genus and share the same overall form and venation patterns with the Scottish species. *T. richardsonii* is similar to *C. arcticum* of Greenland with its more undulating margin type (Kvacek et al. 2004). This indicates that *T. richardsonii* is distinct from *T. antiqua* of Scotland, but may be related to the Greenland forms. *T. crenulata* is most similar to Scottish forms as its teeth are more distinct and developed. The teeth of *T. crenulata*, however, are generally smaller and the tooth sinus is more rounded, which suggests these two species are distinct.

Trochodendroides prestwichii leaves are present in southern England from the Late Paleocene to Early Eocene Reading Beds and Woolwich Beds of the London Clay Formation. The leaves are very abundant, and account for up to 80% of the fossil leaf specimens at some localities (Crane 1984). *T. prestwichii* shares many similarities with *T. antiqua* in terms of its overall shape and size, but does differ in its apex and basal morphology. Specimens of *T. prestwichii* figured by Crane (1984) show that it has a convex or truncate base shape and is unlike the cordate base shapes of the Scottish forms. Boulter and Kvacek (1989) also noted that the apex of *T. prestwichii* was more acute and had an acuminate apex compared to the Ardtun specimens of *T. antiqua*. The differences in apex and base shape suggest that these two British forms of *Trochodendroides* represent two distinct species.

Fossil leaves similar to *Trochodendroides* found in association with fruits, seeds and seedlings from the Late Paleocene of Alberta have provided the most complete insight into early *Cercidiphyllum*-like plants. The combined botanical elements of leaves, inflorescences, seeds and seedlings were assigned to the genus *Joffrea* (Crane and Stockey 1985). Leaves of *Joffrea* at the Joffre Bridge locality are relatively uncommon, although the seeds and seedlings are highly abundant. Crane and Stockey (1985) suggested that this population structure indicated that *Joffrea* was an excellent coloniser of disturbed riparian environments and had an efficient dispersal strategy, but may not have been an ecologically dominant species (Crane and Stockey 1985). Boulter and Kvacek (1989) also suggest that *T.antiqua* may have had a similar ecology to *Joffrea* and may have been a capable coloniser of lava flows and riparian environments of the BTVP.

Foliage of *Joffrea* is broadly similar to *T. antiqua* and other *Trochodendroides* species from the Northern Hemisphere, which provides further evidence that *T. antiqua* is a member of the Cercidiphyllaceae. Tooth structure of *Joffrea speirsii* is significantly different to *T. antiqua*, as some specimens figured by Crane and Stockey (1985) have much smaller teeth and have more rounded tooth sinuses and, the base shape is truncate and different to the cordate base of *T. antiqua* of Scotland.

The distribution of foliage attributed to the Cercidiphyllaceae suggests that this family was common and widespread in the Northern Hemisphere during the Paleocene. Comparisons with *Trochodendroides antiqua* (AM2) and other fossil species of this form genus suggest that the Scottish forms are related to other species in the Northern Hemisphere, but represent a distinct species that appears to be endemic to the BTVP.

3.9.6 Similarities to modern taxa

The leaf morphology of AM2, like other members of the form genus *Trochodendroides*, indicates that it may be an ancestral member of the Cercidiphyllaceae (Crane and Stockey 1986, Boulter and Kvacek 1989). Both the fossil and modern representatives of this family indicate that it shares the same basic leaf form and venation pattern with modern *Cercidiphyllum* which suggests they may have a shared ancestry (Brown 1939, Crane and Stockey 1986, Boulter and Kvacek 1989).

Joffrea from the Early Paleocene of Alberta, Canada has provided some of the strongest evidence for the presence of Paleocene representatives of this family. This plant has been identified as an ancestral genus of the Cercidiphyllaceae based on the preserved reproductive structures and attached foliar elements (Crane and Stockey 1985). *Cercidiphyllum*-like seeds have been identified from interbasaltic sequences of Northern Ireland (Boulter and Kvacek 1989), which suggests that this family was present in the BTVP. Reproductive structures of *Cercidiphyllum*-like plants have not been found in Scottish localities of the BTVP, which prevents a definitive association with the Cercidiphyllaceae. The shared morphological similarity of *Trochodendroides antiqua* of the BTVP with both modern members of the Cercidiphyllaceae and extinct Paleocene forms suggests that it was most likely an ancestral member of this family.

3.10 Angiosperm morphotype 3 (AM3)

3.10.1 Specimen numbers

The specimen numbers of this morphotype are: ACC: 001.a, d, I, 004-b, 007-a, 009, 010-a, 011, 012-a, b, d, 013, AM.NA: 0001-a, i, n, o, r, 002-a, 002-b, 003-a, b, 004-a, b, 006-a, c, 015-a, 019-a, 024, 030, 034, 039-a, 043-a, 048, 049-b, 051-a, 055, 059-c, d, 061-c, 064-a, b, 073, 074, 079-a, 080-a, 082-a, b, 084-b, 084-c, 084-q, 084-x, 089, 095-b, 110-a, 116-a, 124-c, 126-b, 140-a, 141-d, 162, 170-a, 180-a, 185, 200-a, 200-b, 209, 216-a, 222, 227, AM.NA.2008: 001-a, c, 006-d, 011-b, 012-e, 016-b, AM.NA.2009: 004, 011-a, 011-b, 011-d, 011-e, 020-b, 025, 026-b, 033-a, NMS.G.2004.29: 005-b, 008-I, 021-d, 023-e, 023-j, 023-m, 025-d, 028-a, 028-c, 028-e, 047-c, d, g, 050, 051-a, b, 055-j, 061-b, 063-b, 065-a, b, 066-b, 066-i, 081-a, 082-a, 083-a, f, 084, 096-b, 100-a, 2-c, 3-d, 5-g, 5-n.

3.10.2 Diagnosis

Leaf attachment petiolate. Blade attachment marginal, laminar size microphyll to mesophyll, laminar L:W ratio ~1.5:1 – 2:1, laminar shape elliptic, blade medially symmetrical to asymmetrical, base symmetrical or with asymmetrical basal extension, Unlobed, margin serrate. Apex angle acute, apex shape straight or acuminate with a drip tip, base angle reflex or obtuse, base shape cordate or convex. Primary venation pinnate, naked basal veins absent, three or five basal veins, compound agrophic veins. Major secondary veins craspedodromous, interior secondaries absent, minor secondaries craspedodromous, major secondary spacing decreasing proximally, secondary vein angle abruptly increasing proximally, attachment decurrent or excurrent. Intersecondary veins absent. Intercostal tertiary vein fabric opposite percurrent with obtuse vein angle that decreases exmedially. Epimedial tertiaries opposite percurrent, proximal course parallel to intercostals or perpendicular to midvein, distal course parallel to epimedial tertiaries or basiflexed. Exterior tertiary course terminating at the margin. Quaternary vein fabric mixed percurrent, higher order venation not visible. Tooth spacing regular to irregular with up to three tooth orders and 3 teeth/cm. Sinus shape angular, tooth shapes convex/convex, concave/convex, flexous/convex and straight/straight. Principal vein present and terminates at tooth apex, accessory veins unclear but appear looped. Tooth apex simple.

3.10.3 Identification

Angiosperm morphotype 3 (AM3) is the most abundant morphotype in the Allt Mor assemblage and as a result there are many well preserved specimens. The characteristic features of AM3 include its cordate base, acuminate or acute apex, compound serrate margin, pinnate craspedodromous venation, compound agrophic veins and opposite percurrent tertiary veins. Because this morphotype is well preserved it has been possible to identify it as a known fossil taxon, *Corylites hebridicus*.

Fossilised leaves of *Corylites hebridicus* are an abundant component of the Ardtun leaf beds (Boulter and Kvacek 1989), and show a striking similarity to AM3 as both leaf types share the same characteristics mentioned previously. In addition to this shared morphological resemblance, leaves from both localities display a high degree of variation. This morphological variability is usually expressed in the overall size of the laminar, its length:width ratio, apex and base shape and tooth characteristics. The morphological variability of AM3 is discussed in greater detail in section 3.10.4.

The leaves of *Corylites hebridicus* of Ardtun, Mull and AM3 of Skye are almost indistinguishable morphologically. This indicates that AM3 represents the same species as those of Ardtun and is regarded as *Corylites hebridicus*. The high abundance of this taxon in the leaf assemblages of Mull and Skye may indicate that this was important component of BTVP vegetation during the mid Paleocene.

3.10.4. Discussion

The abundance and good preservation of AM3 has enabled a detailed understanding of its morphological features and how they vary between specimens. Multiple well preserved specimens have provided information on the overall laminar form, venation and margin (e.g.

ACC.001-a, ACC.012-b, ACC.012-d, AM.NA.2008.012-b, AM.NA.2008.016-b, AM.NA.073) (Figures 3.19, 3.20). These specimens have enabled other poorly preserved specimens to be identified to this morphotype.

The leaves of this morphotype are petiolate and their attachment is marginal. The petiole is quite long and ranges from ~20mm to 50mm. Petiole preservation is relatively rare but provides some indication as to how the leaves were attached to the parent plant. Laminar size varies considerably and estimates of the original size of the specimens indicates that they range from 800 mm^2 (microphyll) to in excess of 8000 mm^2 (mesophyll). The most complete specimens (e.g. Acc-001-a, Acc-012-b, AM.NA.2008.016-b, AM.NA.2008.016-b, AM.NA.2009.007-a, AM.NA.0164-a) range from 1907 mm^2 to 5349 mm^2. The most common size class of leaves that can have their original size determined from measurements of their preserved area or specimens whose original area can be estimated straddle the upper range of microphyll to the lower range of notophyll.

Laminar length:width ratio, like laminar size, is difficult to determine for the majority of the specimens due to fragmentation. Some specimens (e.g. Acc 001-a, AM.NA.2008.016-a, b, AM.NA.0015-a) have ratios of ~1.7-2:1 (Figures 3.19-a, 3.20-b). Some of the larger specimens appear to be broader (e.g. ACC.012-b, AM.NA.073, AM.NA.011-a, b) (Figures 3.19-b, 3.20-e), but estimating their L:W ratios is more difficult to calculate as they are missing apexes. To estimate the original L:W ratio of these specimens the length of the specimen was estimated by using the curvature of the proximal margin as guide to the original length. If these estimates are accurate it suggests that some of the leaves had L:W ratios of ~1.2-1.5:1. Comparisons with the Mull specimens indicates that their L:W ratio varies to a similar degree as those of Skye. The variation in laminar size and L:W ratio may be due to leaf ontogeny (young or mature leaves) or may caused by environmental factors such as growth position and light intensity, which may influence leaf form (Upchurch and Wolfe 1987).

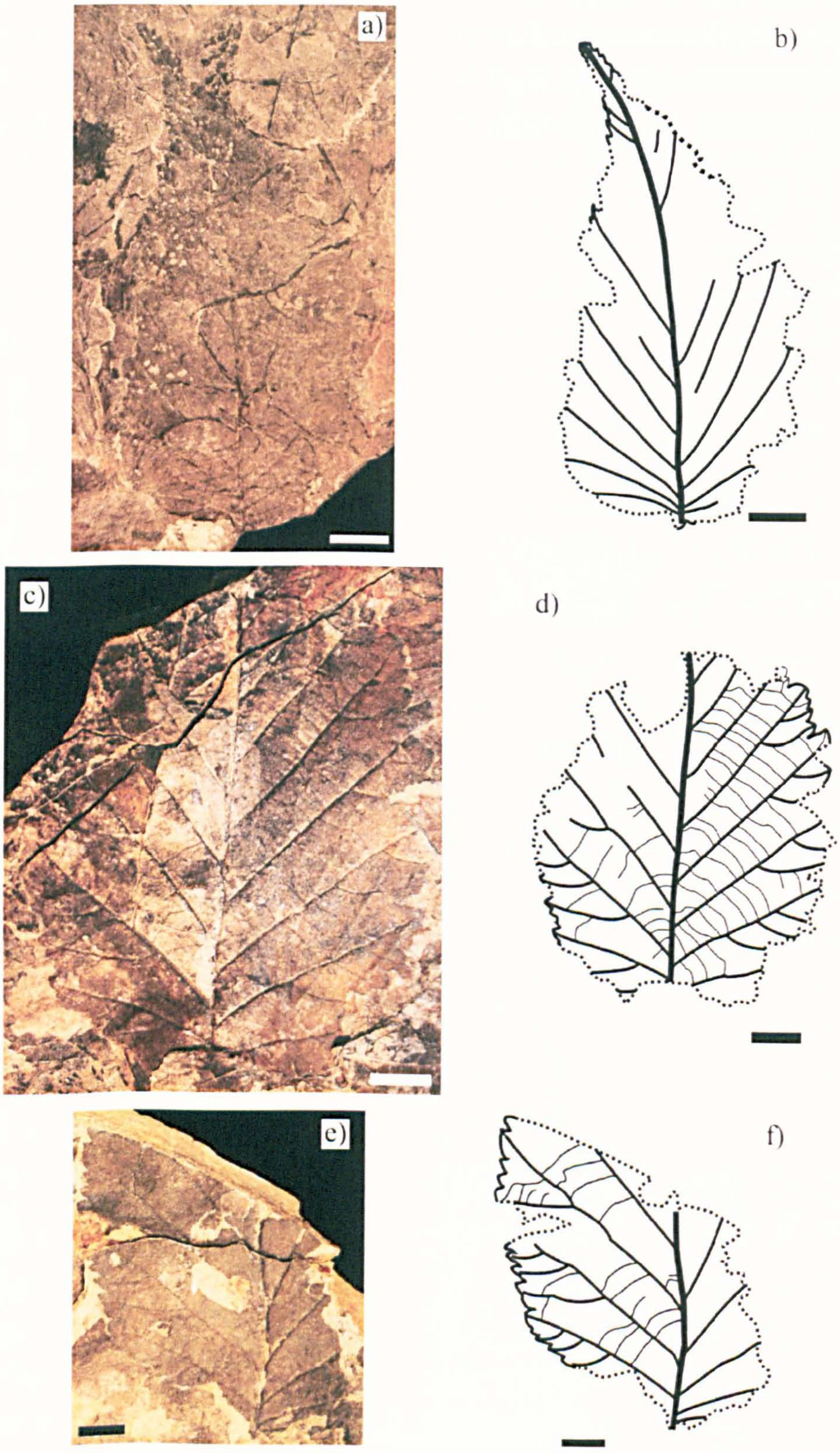

Figure 3.19. Well preserved specimens of AM3. a) ACC.001-a, b) line drawing of ACC.001-a, c) ACC.012-b, d) line drawing of ACC.012-d, e) ACC.012-d, e) line drawing of ACC.012-d. Scale bars = 1 cm.

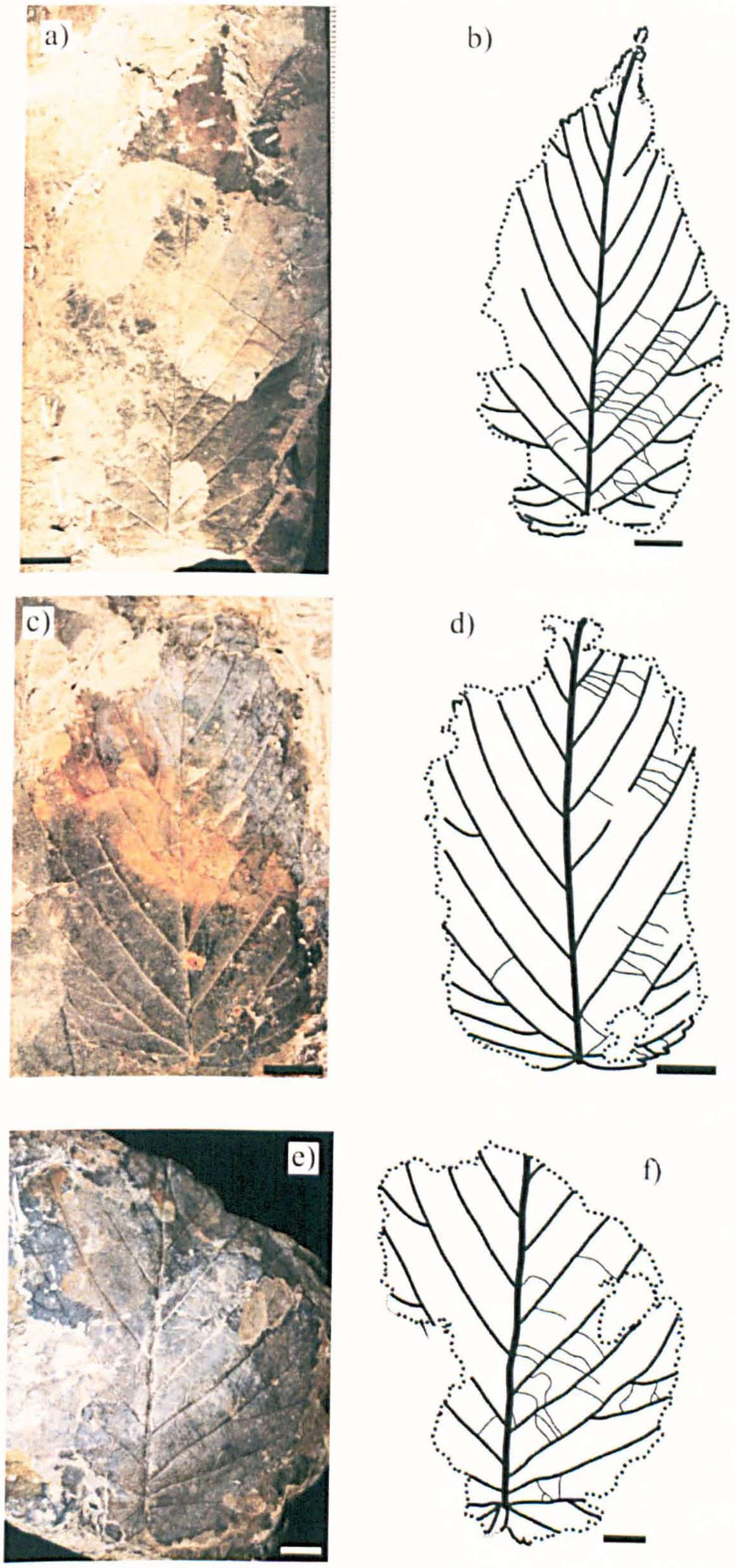

Figure 3.20. Well preserved specimens of AM3. a) AM.NA.2008.016-b, b) line drawing of AM.NA.2008.016-b, c) AM.NA.2008.012-b, line drawing of AM.NA.2008.012-b, e) AM.NA.073, f) line drawing of AM.NA.073. Scale bars = 1cm.

All specimens with preserved apexes have acute apex angles that range from 40 ° to 63°. The acuteness of this angle is linked to the apex shape, which is either straight or acuminate. Leaves with straight apex shapes (e.g. AM.NA. 19, AM.NA. 40-b, AM.NA. 180) have less acute apex angles that are ~50 ° (Figure 3.21-a). Leaves with acuminate apex types (e.g. Acc.001-a, AM.NA.2008.016-b) have more acute apex angles that range from 40 ° to 50 ° (Figures 3.19-a, 3.20-a, 3.21-c, e). The shape of the acuminate apex can be either hooked or forming a drip tip. Leaves with hooked acuminate apexes have one flank that is straight or partially convex and another flank that is concave (e.g. NMS.G.2004.29.025-d, NMS.G.2004.29.060) (Figure 3.21-c, e). The distal section of the laminar curves away from the midvein and abruptly narrows and extends for ~5 mm to 10mm in specimens with acuminate apexes that form drip tips (e.g. ACC.001a, AM.NA.2008.016-b) (Figures 3.19-a, 3.20-a).

Base angles are either reflex or are obtuse, and like apex angle, are linked to base shape. Leaves with reflex angles have a cordate base shape, while those with more obtuse angles have a convex base shape (e.g. AM.NA.001-a) (Figure 3.22-a). Leaves with cordate bases are the most common, but the depth and width of the basal sinus varies. Some specimens have relatively weakly developed cordate base shapes (e.g. AM.NA.2008.016-b, AM.NA.0015-a), i.e. the sinus is short and narrow, while others (e.g. AM.NA.004-b, AM.NA.073, AM.NA.089-b) have very broad and deep sinus (Figures 3.20-a, 3.20-e, 3.22-c, e).

The lower order venation of AM3 is pinnate craspedodromous with compound agrophics that have a craspedodromous course. The course of the secondaries is typically straight but can be straight-curved, weakly curved or sinuous. All leaves have compound agrophics but the abundance of these veins and the extent they occur higher up the laminar varies. The agrophic veins are most numerous and tightly spaced in the most basal part of the laminar and are derived from the lowest pair of secondary veins. The number of agrophics then decreases further up the laminar. Some specimens (e.g. ACC.012-a, ACC.012-b AM.NA.073, AM.L4.08.0003-a) have agrophics high up in the laminar, while others (e.g. AM.NA.089-b, AM.UN.08.0003-a) only have them in the proximal-middle portion of the laminar.

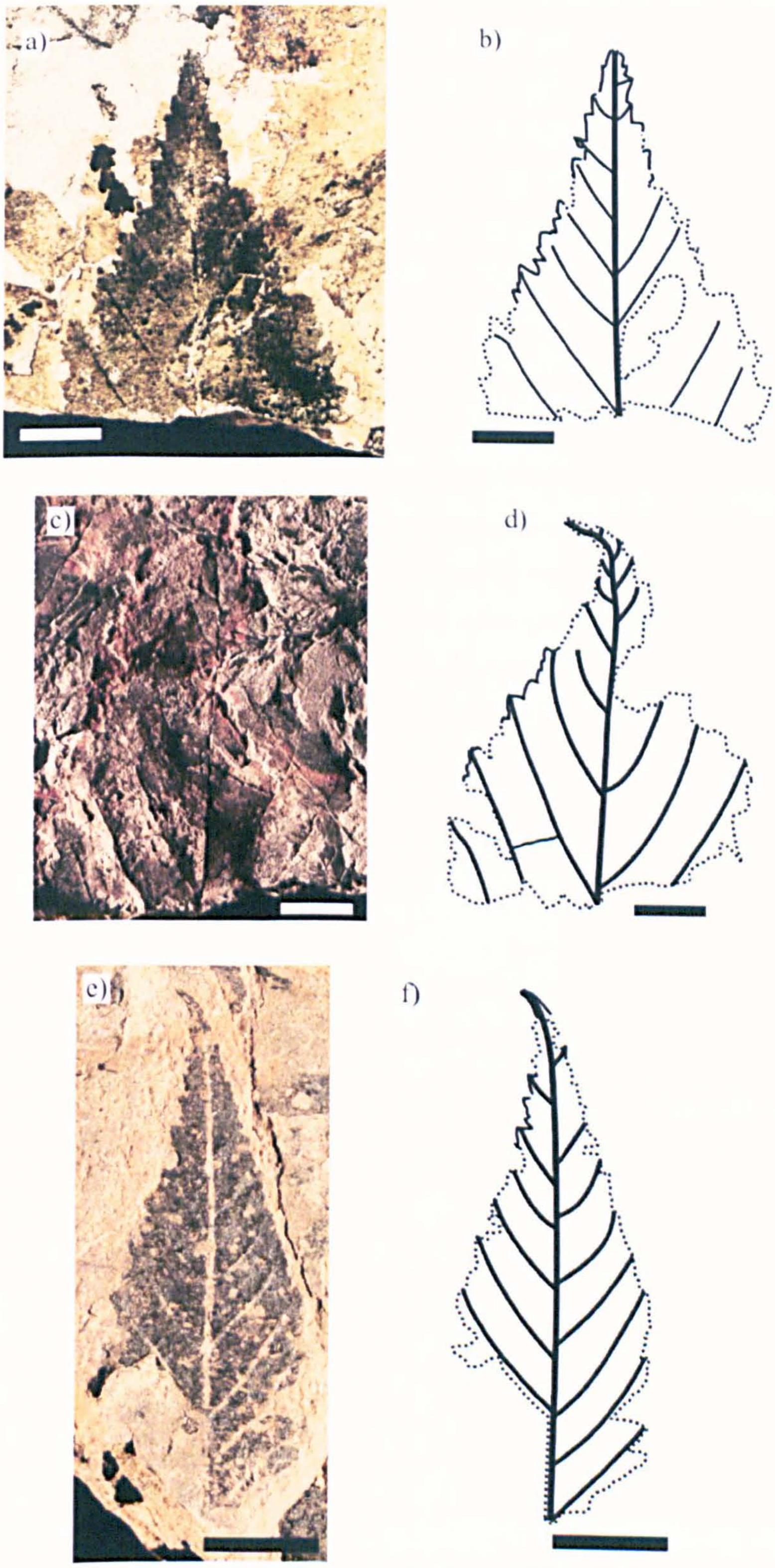

Figure 3.21. Examples of leaf apexes of AM3. a) AM.NA.019-a, b) line drawing of AM.NA.019-a, c) NMS.G.2004.29.025-d, d) line drawing of NMS.G.2004.29.025-d, e) NMS.G.2004.29.060, f) line drawing of NMS.G.2004.29.060. Scale bars = 1 cm.

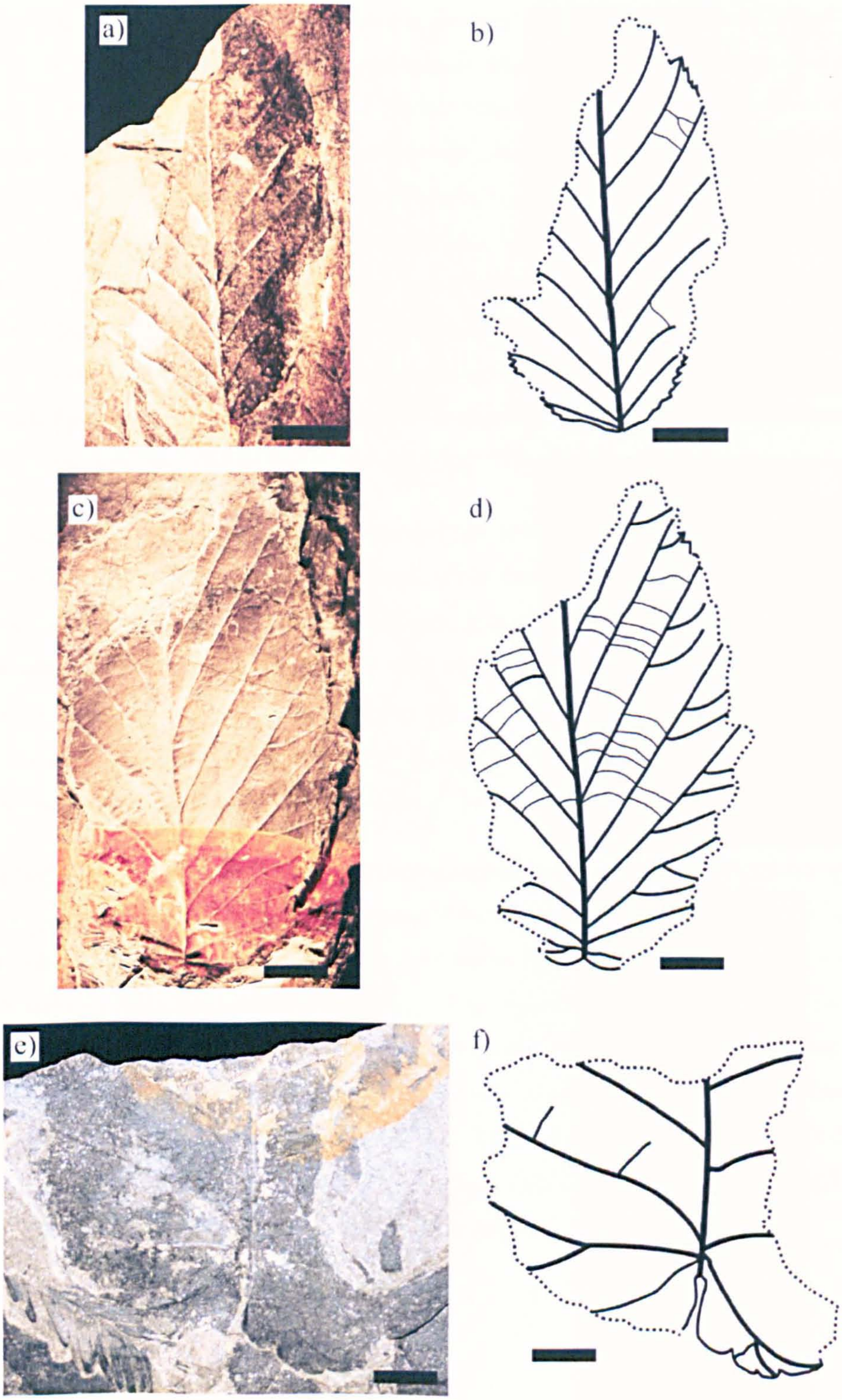

Figure 3.22. Specimens of AM2 showing variations in base shape a) AM.NA.001-a, b) AM.NA.001-a, c) AM.NA.015-a, d) line drawing of AM.NA.015-a, e) AM.NA.004-b, f) line drawing of AM.NA.004-b. Scale bars = 1 cm.

Secondary vein frequency is high in AM3 and the secondary veins are often tightly spaced, with between 12 to16 pairs major secondary veins present. The secondary veins appear relatively evenly spaced in the middle section of the laminar, but become more tightly spaced proximally. In the most basal section of the laminar near the petiole the veins may only be a few millimetres apart. The secondary veins in the middle section of the laminar are fairly uniform with vein angles of ~30 ° to 35 °, but increase abruptly towards the base of the laminar with the most proximal basal veins having angles that range from ~70 ° to 90 °.

The intercostal tertiary veins are opposite percurrent, occasionally forked with straight, convex or sinuous courses. The intercostal tertiary veins are obtuse to the midvein and decrease exmedially. Admedially intercostals vein angle ranges from 120 ° to 150 ° and exmedially ranges from ~100 ° to 130 °, which indicates intercostals vein angles increase exmedially. Intercostal vein angles in the basal section of the laminar indicates that intercostals vein angle also decreases proximally. The epimeidal tertiary veins are opposite percurrent and have variable proximal and distal courses. The proximal course can be either parallel to the intercostal tertiary veins or perpendicular to the midvein. The distal course can be parallel to the intercostals or basiflexed. The exterior tertiary veins typically terminate at the margin where they form the principal veins of teeth, or join the tooth sinus. Quaternary vein fabric is not well represented but appears to be mixed percurrent. Higher order venation and aerolation is unclear due to limited preservation.

The margin of AM3 is distinctive, even very small fragments with margin preserved can be readily attributed to this morphotype. The teeth can be regularly spaced (e.g. AM.NA.019, ACC.012-b), or irregularly spaced (e.g. Acc.012-d) (Figures 3.19-c, e). Most specimens with margin preservation have compound teeth with three tooth orders. The first tooth order is primarily supplied by the major primary veins, the second order by agrophics or branches of the major secondaries and the third order teeth are supplied by the tertiary veins. Tooth sinus shape is uniformly angular, but the width of the sinus is variable.

Perhaps the most variable characteristic of this morphotype is tooth shape, as tooth shape can vary even within the same specimen (e.g. ACC.012-b). The most common tooth shapes are convex/convex and concave/convex, but flexous/convex and straight/straight as well combinations of these are present. Tooth shape also varies in different parts of the laminar: along the basal margin the teeth are simple (one order) and have convex/convex or concave/convex shapes, with longer proximal flanks relative to distal flanks. Teeth derived from the margin along the leaf apex become less compound and have straighter distal and proximal flanks, which gives the teeth a triangular appearance (e.g. ACC.001-a, AM.NA.2008.016-b). Each tooth is supplied by a principal vein that terminates at the tooth apex, it can be derived from either major secondary veins, agrophics or marginal tertiary veins. The apex of the teeth appears simple with no visible glands or projections.

3.10.5 Similarities with other fossil taxa

Fossil leaves of *Corylites* indicate that it was an abundant and important component of Paleocene floras of Northern Hemisphere and occurs in both high and mid latitude sites in North America, Europe, Asia and the Arctic (Laurent 1912, Crane 1981, Sun and Stockey 1992, Manchester and Chen 1996, Manchester and Guo 1996, Gemmil and Johnson 1997, Manchester and Chen 1998, Wilf et al. 1998, Collinson and Hooker 2003, Manchester et al. 2004, Herman 2007a, Herman 2007b, Herman 2007c, Herman et al. 2009, Moiseeva 2009, Moiseeva et al. 2009, Hao et al. 2010). The broad latitudinal and longitudinal range of this leaf type in the Paleocene suggests it was an excellent disperser and coloniser, and based on its latitudinal range it appears to be tolerant of a broad range of climates.

The distribution of *Corylites hebridicus* is not restricted to the BTVP as leaves of this taxon have been described from the Early Paleocene of Greenland and the Paleogene of Svalbard (Koch 1963, Kvacek et al. 1994). Figured specimens from both sites indicate both leaf types share the same characteristic morphology as Scottish forms. This indicates that this plant species was common in the Brito-Arctic region in the Early and mid Paleocene.

The Paleocene European record of betulaceous foliage includes localities from southern England and France. Betulaceous leaves have been identified from the Upper Paleocene Reading Beds in southern England (Crane 1981). The foliage is found in association with infructescences of *Palaeocarpinus laciniata*, which indicates a betulaceous affinity for the leaves (Crane et al. 1981). The leaves were designated to the form genus *Craspedodromophyllum*, which are distinct from the leaves of *Corylites*. The base shape is acute, are typically or rarely compound with straight sided flanks.

Two species of Betulaceae-like foliage were figured by Laurent (1912), *Corylus macquarrii* and *Alnus palaeoglutinosa* from the mid Paleocene of Menat, France. The specimens of *Corylus macquarrii* are identical to *Corylites*, and the other betulaceous species at Menat *Alnus palaeoglutinosa* is probably a smaller representative of *C. macquarrii*. It is likely that these leaf species are *Corylites hebridicus*, which was suggested by Boulter and Kvacek (1989) to be the case.

North American Paleocene records of *Corylites* foliage are extensive and several sites have associated reproductive structures preserved with the leaves. The infructescences of several species of the extinct betulaceous genus, *Palaeocarpinus* have been found in numerous localities in the western United States and Canada, and are often associated with *Corylites*-like leaves (Sun and Stockey 1992, Manchester and Chen 1996, Manchester and Chen 1998, Manchester et al. 2004). *Palaeocarpinus joffrensis* from the Early Paleocene Paskapoo Formation, Alberta are found in association with betulaceous leaves (Sun and Stockey 1992). The leaf specimens figured by Crane and Stockey (1992) do appear broadly similar to *Corylites hebridicus* as they have similar teeth and venation, but differ in that they have fewer, more widely spaced secondary veins and have a convex base shape.

Palaeocarpinus aspinosa had a wide distribution in the western United States during the Paleocene with occurrences in Wyoming, Montana and North Dakota (Manchester and Chen 1996). Fossil leaves attributed to *Corylites* occur with these reproductive structures. The figured specimens in Manchester and Chen (1996) are similar to the Scottish forms but have smaller teeth, a lower number of secondary veins that are widely spaced and have weakly developed cordate sinuses.

Another species of *Palaeocarpinus*, *P. dakotensis* has been described with associated *Corylites* foliage from the Paleocene of North Dakota (Manchester et al. 2004). The *Corylites* foliage associated with this species of *Palaeocarpinus* is most like the Scottish forms in its overall leaf from, venation and tooth structure. It can, however, be differentiated from *Corylites hebridicus* by its much shorter apex, and in one specimen figured by Manchester et al. (2004) near-lobate margin.

A second genus of the Betulaceae was present in North America during the Paleocene. *Cranea*, which has foliage of *Corylites* associated with it (Manchester and Chen 1998). The various reproductive structures associated with *Cranea* share characteristics with most modern genera of the Betulaceae but it is regarded to be most similar to extant members of *Ostryopsis* (Manchester and Chen 1998). The associated *Corylites* foliage, like those associated with *Palaeocarpinus,* is unlike the Scottish forms. The leaves figured by Manchester and Chen (1998) have rounded or weakly developed cordate bases, and a greater number of secondary veins.

The Betulaceae were not just diverse in the Paleocene of North America but were dominant members of many plant assemblages. Leaves of *Corylites* often dominate many of the floras from the Early to mid Paleocene Fort Union Formation of Wyoming where they account for ~38% of leaves recovered (Gemmill and Johnson 1997). Similar leaf abundances for *Corylites* were reported from the Late Paleocene of Wyoming, where they also dominate the plant assemblages (Wilf et al. 1998).

Corylites leaves are also present in Paleocene sequences in Asia and indicate that they had a similar diversity and abundance to Europe and North America during this interval, the leaves are also associated with *Palaeocarpinus* infructescences (Manchester and Guo 1996, Herman

2007a, Herman 2007b, Herman et al. 2009, Moiseeva 2009, Moiseeva et al. 2009). Leaves of *Corylites beringianus* are a major component of Paleocene floras across north eastern Russia and Alaska (Herman 2007a, Herman 2007b, Herman 2007c, Herman et al. 2009, Moiseeva 2009, Moiseeva et al. 2009). *Corylites beringianus* leaf form indicates that is more similar to *Corylites hebridicus* than many of the North American taxa. Despite the close similarity in many of the character traits it is apparent that these two taxa are distinct. Figured specimens of *C. beringianus* show it has a much broader basal sinus and in some specimens appears near lobate. Paleocene leaves associated with *Palaeocarpinus orientalis* in China are very similar to leaves of *C. hebridicus*, some specimens figured by Manchester and Guo (1996) look similar to some of the smaller specimens from Ardtun. The Chinese foliage is, however, distinct, as they have fewer secondary veins and the teeth on the larger specimens are smaller and more rounded.

3.10.6 Similarities with modern taxa

The leaves of *Corylites hebridicus* are characteristic of the Betualceae in their overall form and venation patterns. The leaves of this morphotype most closely resemble leaves of modern *Corylus*, as their name implies. Based solely on foliar features it appears *Corylites hebridicus* of the BTVP is a member of the Betulaceae.

Betulaceae inflorescences (*Paleocarpinus*) are often found in association with *Corylites* leaves (Crane and Stockey 1992, Manchester and Chen 1996, Manchester and Guo 1996, Manchester and Chen 1998, Manchester et al. 2004). The morphology of *Paleocarpinus* inflorescence suggests they are related to several modern genera while the associated leaves resemble *Corylus* (Crane and Stockey 1992, Manchester and Chen 1996, Manchester and Chen 1998, Manchester et al. 2004).

The presence of character traits associated of several modern genera within the same inflorescence, and the relatively consistent morphology of the leaves associated with these inflorescences indicates that the different plant organs within the Betulaceae evolved at different rates (mosaic evolution). The presence of morphological characters that occur in several modern genera indicate that the Betulaceae was in its early stages of evolution during the Paleocene, and had not yet diversified into distinct modern genera during this interval.

The leaves of *Corylites hebridicus* from Skye and Mull indicate that the parent plant was a member of the Betulaceae. This family association is not unequivocal as no specimens of *Paleocarpinus* inflorescence have been found in the BTVP. *Corylites* leaves found in association with *Paleocarpinus* inflorescences at other localities suggests that these leaf types and the inflorescence represent the same plant species. The close resemblance of the BTVP leaves with those found in association with betulaceous inflorescences indicates that Corylites hebridicus is a member of the Betulaceae. Without associated inflorescences coupled with the undifferentiated nature of this family in the Paleocene it impractical to assign AM3 to a modern genus. *Corylites hebridicus* is therefore considered as an archaic member of the Betulaceae with an unknown generic affinity.

3.11 Angiosperm Morphotype 4 (AM4)

3.11.1 Specimen numbers

The specimen numbers of this morphotype are: ACC: 006, 0014, AM.NA.001-b,d, 006-b, 016-a, 061-a, 084-a, 099, 109-a, 164-a, AM.NA.2008.016-a, NMS.G.2004.29: 015-c, 019-a, 047-e, f, 072-b, ACC.AM.032-b.

3.11.2 Diagnosis

Blade attachment marginal, laminar size microphyll to notophyll, laminar L:W ratio ~2:1, laminar shape elliptic, Medially asymmetric, base possibly asymmetrical, unlobed, margin serrate. Apex angle acute, apex shape unclear acute and or acuminate with a drip tip, base angle unclear obtuse and or reflex, base shape unclear convex and or cordate. Primary veination pinnate, naked basal appear veins absent, three to five basal veins, compound agrophic veins. Major secondary veins craspedodromous, interior secondary veins absent, minor secondary veins craspedodromous, major secondary spacing decreasing proximally, secondary angle increasing abruptly proximally, major secondary attachment excurrent or proximally decurrent. Intersecondary veins absent. Intercostal tertiary vein fabric opposite percurrent with obtuse vein angle that increases proximally. Epimedial tertiary veins opposite percurrent with proximal course parallel to intercostal tertiary veins or perpendicular to the midvein and distal course parallel to intercostals or basiflexed. Exterior and higher order venation not visible. Tooth spacing regular or irregular, with two orders of teeth and 2 to 3 teeth/ cm, sinus shape angular. Tooth shapes convex/convex, straight/convex and concave/convex. Principal vein present with termination at tooth apex.

3.11.3 Identification

Angiosperm morphotype 4 (AM4) overall form and venation pattern are similar to AM3 (see section 3.10), but is distinguished from this other morphotype by differences in medial symmetry, margin, base form and secondary veins. Specimens of AM4 are typically medially asymmetric; this is not a unique feature of this morphotype as AM3 also display this characteristic. The degree of asymmetry however, appears to be greater for AM3, but the precise differences between the two sides of the laminar cannot be determined due to the fragmentation of the specimens.

The margins of both AM3 and AM4 are broadly similar but the teeth of AM3 are typically more rounded or triangular in shape compared to AM4, which often has a more prominent projection of the tooth apex. The base shape of AM4 is partially preserved in several specimens but is not complete, but appears to be more rounded and possibly asymmetric compared to AM3.

Perhaps the most distinguishing feature that differentiates the two morphotypes is the anatomy of the secondary veins. The major secondary veins of AM4 develop significant branches and or forks. The major secondary veins that are forked bifurcate near to the margin, which is rare or altogether absent in AM3. These differences in morphology are consistent enough to warrant their differentiation into two morphotypes.

The close morphological resemblance of AM4 with AM3 suggests that it is a related species, and possibly another form of *Corylites*. The secondary vein branches and forking at the ends of the secondary veins, however, may indicate that this morphotype is related to family Ulmaceae. The genus *Ulmus* within the Ulmaceae is similar to both *Corylites* and modern Corylus (Betulaceae) in its overall form and venation patterns, but has secondary vein forks and prominent secondary vein branches that are similar to AM4. This may suggest that AM4 is *Ulmus* relative, AM4 was compared to Paleogene representatives of the Ulmaceae to determine if it is member of this family or another betulaceous leaf type.

Specimens of *Ulmites ulmifolius* from the Paleocene and Eocene plant assemblages of Svalbard indicate that the two leaf types share some common features (Kvacek et al. 1994). Both leaf types have quite broad compound teeth, forked secondary veins and tightly spaced intercostal tertiary veins. The leaves of *Ulmites ulmifolius* are, however, unlike those of AM4 as the laminar is narrower, less asymmetric, the secondary vein forks are more frequent and they appear to lack agrophic veins.

Ulmus okanaganensis from the mid-late Eocene of British Colombia displays significant polymorphism with its foliage, and some of these morphs are similar to AM4 (Denk and Dillhoff 2005). The larger, possibly sucker foliage is very similar to AM4 as the secondary veins forks develop further from the margin, the primary teeth are much larger than secondary teeth, and they posses agrophic veins. The smaller leaves of *Ulmus okanaganensis* are very similar to the smaller leaf specimens of *Ulmites ulmifolius*, which suggests polymorphism of ulmaceous foliage was prevalent in the early Paleogene. Leaves similar to the small leaves of *Ulmites ulmifolius* and *Ulmus okanaganensis* have not been observed in the Allt Mor assemblage. The absence of these leaf types may suggest that AM5 is not a representative of the Ulmaceae, or simply that these leaves have not been discovered or preserved within the assemblage. Another characteristic feature of *Ulmites ulmifolius* and *Ulmus okanaganensis* is their petiole, which is short and thick, which is typical of modern *Ulmus* (Denk and Dillhoff 2005). Petioles of AM4 have not been observed, so it is not certain if the Skye leaves shared this feature.

Two specimens of *Corylites hebridicus* from Ardtun figured by Boulter and Kvacek (1989) (V.26316 and V.25109) appear similar to AM4 as they have prominent vein branches and forked secondary veins. These specimens may have been misidentified, and may potentially represent a distinct species that is comparable to AM4. Boulter and Kvacek (1989) extracted and analysed cuticle from V.26316 to determine its affinity more comprehensively, the cuticle extracted was poorly preserved and thin, but showed features, particularly of stomatal morphology that are similar to the Betulaceae. The absence of Ulmaceae-like pollen from the BTVP (Jolley 1997, Jolley et al. 2009) also suggests that AM4 is not a member of the Ulmaceae.

The morphology of AM4 suggests it may either represent a member of the Ulmaceae or the Betulaceae. Evidence from leaf cuticles from Ardtun, the BTVP palynomorph record and shared morphological features of *Corylites hebridicus* indicates that AM4 is more likely a representative of the Betulaceae. The close similarity to *Corylites hebridicus* suggests that AM4 may represent another related species, and is regarded as "*Corylites* cf.". This identification is tentative, however, as the leaves of AM4 are still similar to the Ulmaceae. Additional specimens with attached petioles and cuticular preservation are required to conclusively demonstrate its relationship with either the Betulaceae or Ulmaceae.

3.11.4 Discussion

The morphology and variation in leaf form of AM4 is relatively well understood as several well preserved specimens are present in the collection (e.g. AM.NA.001-d, AM.NA.016-a, AM.NA.061-a, AM.NA.109-d, AM.NA.164-a, ACC.003-c) (Figures 3.23 and 3.24). The original laminar size can be estimated for some specimens (e.g. AM.NA.001-d, AM.NA.0061-a, AM.NA.109-d) due to their lower levels of fragmentation and margin preservation. Laminar size ranges between 1277 mm^2 to 3073 mm^2, which indicates that the leaves fall within the microphyll to notophyll size classes. Laminar length:width ratios for some specimens (e.g. AM.NA.061-a, AM.NA.109-a, ACC.003-a) can be estimated and indicate that L:W ratios of the leaves are ~2:1 to 2.5:1. Laminar shape appears to be uniformly elliptic.

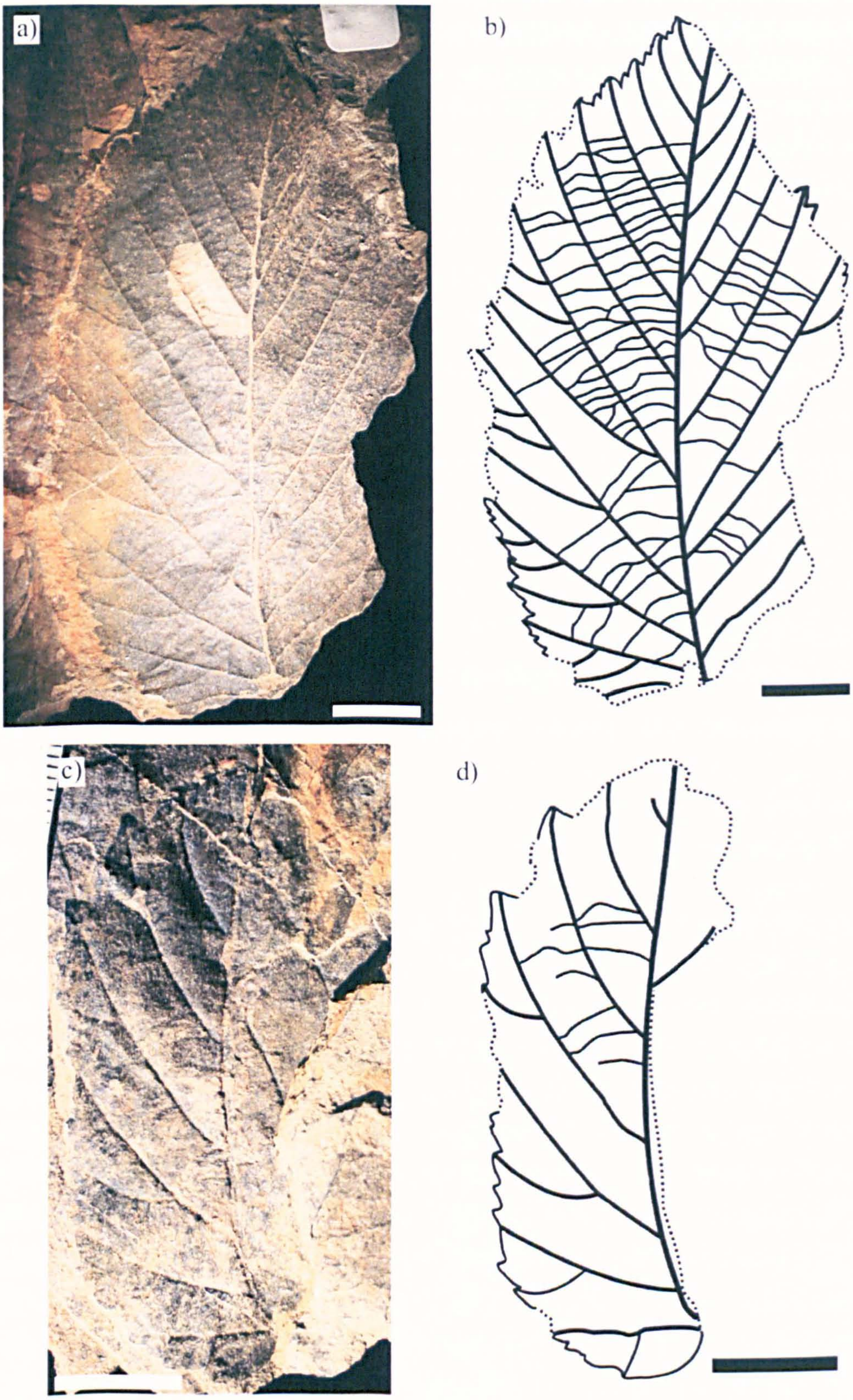

Figure 3.23. Specimens of AM4. a) AM.NA.061-a, b) line drawing of AM.NA.061-a, c) AM.NA.001-d, d) line drawing of AM.NA.001-d. Scale bars = 1 cm.

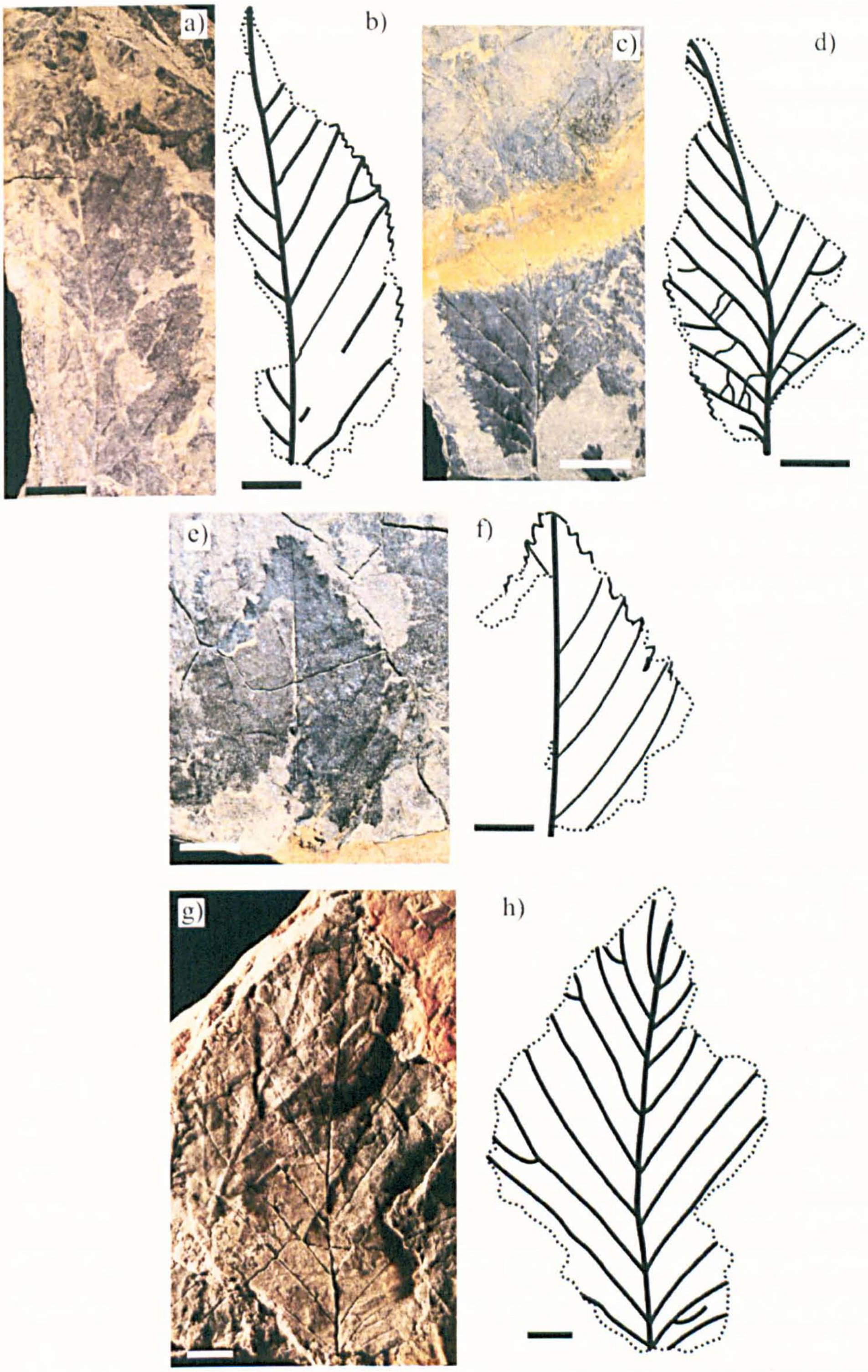

Figure 3.24. Specimens of AM4. a) AM.NA.109-a, b) line drawing of AM.NA.109-a, c) ACC.003-c, d) line drawing of ACC.003-c, e) AM.NA.016-a, f) line drawing of AM.NA.016-a, g) AM.NA.164-a, h) line drawing of AM.NA.164-a. Scale bars = 1 cm.

The apex of AM4 is partially preserved and indicates that its shape was either straight (e.g. AM.NA.016-b) or acuminate (AM.NA.109-a, ACC.003-c). The base shape of AM4 is unclear due to the partial preservation of this feature, but may be either cordate (e.g. AM.NA.001-d) or convex (e.g. ACC.003-c) (Figures 3.23-c and 3.24-c). Basal symmetry is also unclear, but in at least one specimen, (AM.NA.001-d) the curvature of the midvein and partially preserved basal margin indicates that it may have been asymmetric (Figure 3.23-c).

Major secondary vein angles are acute to the midvein and range from 30 ° to 40 ° in the central section of the laminar and increase abruptly towards the base where angles range from of 30 ° to 70 °. Secondary vein branches and forks are characteristic feature of this morphotype and set it apart from the other leaf types from Skye. The secondary vein branches diverge from the major secondary veins between 25 to 50% of their length and have a course similar to that of the major secondary. The secondary vein forks diverge nearer to the margin and form principal veins for the first order teeth (Figure 3.23-a ,b, 3.24-a.)

The intercostal tertiary veins are opposite percurrent and have a variable course that can be either straight, convex or sinuous (Figure 3.23-a). The angle of the intercostal tertiary veins is obtuse to the midvein and increases proximally. Admedial intercostal vein angles range from 97 ° to 130 °, but angles of ~120 ° are more typical. Exmedially the intercostal vein angles increase slightly but proximally they are most obtuse to the midvein, with a range of 140 ° to 150 °. The epimedial tertiaries are opposite percurrent and have variable proximal courses that can be either parallel to the intercostal tertiary veins or perpendicular to the midvein. The distal course appears to be consistently parallel to intercostal tertiaries.

Tooth spacing appears to be relatively uniform, and there are between 2 to 3 teeth/cm. There are two teeth orders, which is unlike AM3, which has up to three orders of teeth. Both tooth orders have similar shapes that can be either concave/convex or convex/convex, sinus shape appears to be consistently angular (Figures 3.23-a, 3.24-a, e). The teeth are supplied by a principal vein that terminates at the tooth apex. The first orders teeth are supplied by the ends of major secondary veins, agrophics, vein branches or forks, the second order teeth appear to be primarily supplied by tertiary veins.

3.11.5 Similarities with other fossil and modern taxa

The taxonomic affinity of AM4 as discussed in section 3.11.3 revealed that its systematic position is uncertain as it may represent a species of the Betulaceae or Ulmaceae. The morphological features and floral record of the BTVP indicated that AM4 is more likely a species of *Corylites* that is distinct from *C. hebridicus*. If AM4 is, indeed, a species of *Corylites* then its similarities to other fossil and modern taxa is likely similar to that of AM3 (see sections 3.10.5 and 3.10.6). If AM4 is a member of the Ulmaceae it may have Paleogene relatives that occur in Svalbard, Canada and China, which appear to be related to modern genera such as *Ulmus* and *Zelkova* (Kvacek et al. 1994, Feng et al. 2003, Denk and Dillhoff 2005, Wang et al. 2010). Additional specimens with cuticular preservation are required to resolve the systematic position of AM4, and until such specimens can be collected it will remain tentatively as "*Corylites* cf.".

3.12 Angiosperm morphotype 5 (AM5)

3.12.1 Specimen numbers

The specimen numbers of this morphotype are: ACC.004-c, AM.NA.082-e, AM.NA.109-a.

3.12.2 Diagnosis

Laminar size microphyll, laminar shape unclear possibly elliptic, blade appears medially symmetric, unlobed, margin serrate. Apex not preserved, base angle appears to be acute, base shape unknown. Primary venation pinnate, agrophic veins absent. Major secondary veins craspedodromous, interior veins absent, minor secondary veins absent, major secondary spacing appears regular, secondary angle decreasing proximally, major secondary attachment proximally decurrent. Intersecondaries absent. Tertiary and higher order vein fabric not visible. Tooth spacing regular, one order of teeth, two teeth per/cm, sinus shape angular. Tooth shape convex/straight to straight/straight. Principal vein present with termination at the tooth apex. Tooth apex appears simple.

3.12.3 Identification

Angiosperm morphotype 5 (AM5) is composed of three poorly preserved leaf specimens. Despite of these low numbers there is sufficient morphological features present to identify this morphotype to a known fossil taxon, *Fagopsis groenlandica*. This morphotype is attributed to *Fagopsis groenlandica* as it has the same secondary vein characteristics and tooth form. Specimens of *Fagopsis groenlandica* from Ardtun, Mull are well preserved and appear similar to AM5. The margin of both leaf types is markedly similar, as they both have convex/convex to straight/straight tooth shapes, angular tooth sinuses, proximal flanks that are two to three times longer than the distal tooth flank and have principal veins that terminates at the tooth apex.

The secondary venation characteristics are also similar and both leaf types share the same numerous, uniformly spaced, nearly straight course, acute angled craspedodromous veins with proximally decurrent attachment. The absence of agrophic veins and intersecondary veins is another feature these leaf types share. Secondary vein angles of AM5 in the central half of the laminar range from 40 ° to 50°. These secondary vein angles are consistent with the Ardtun specimens (Boulter and Kvacek 1989).

The strong similarity between AM5 and *Fagopsis groenlandica* indicates that this morphotype is represents the same plant species. The genus *Fagopsis* was applied to leaves with attached inflorescences; therefore disarticulated leaves without the attached inflorescences cannot be attributed to this genus (Manchester 1999). Leaves with a similar form to *Fagopsis* have been reclassified to a different form genus, *Fagopsiphyllum* (Manchester 1999). The lack of attached or associated inflorescences within the leaf assemblages of the BTVP prevents an association with *Fagopsis*, instead the leaves from Ardtun and those of Allt Mor should be regarded as *Fagopsiphyllum groenlandica*.

3.12.4 Discussion

The three leaf specimens that comprise this morphotype have been assigned to AM5 based on their secondary venation patterns (ACC.004-c, AM.NA.082-e, AM.NA.109-a) and their tooth morphology (excluding AM.NA. 109-a) (Figure 3.25). The original size of the leaf specimens is difficult to determine due to the high degree of fragmentation. The least fragmented specimens of this morphotype, (ACC.004-c and AM.NA.109-a) have laminar areas of 620 mm^2 and 1057 mm^2 respectively (Figure 3.25-a, c). These area measurements are based on the fragmented perimeter of the specimens, and are therefore lower than the original area of the leaf. The laminar area estimates and the section of the laminar these fragments represent indicate that the leaves were originally microphyll to notophyll prior to their fragmentation. Laminar shape is equally difficult to gauge, the curvature of the margin of ACC.004-c indicates the original leaf may have been elliptic but this is tentative.

The secondary veins of AM4 are perhaps its most distinctive feature and were used to identify this morphotype as *Fagopsiphyllum groenlandica* (Figure 3.25). Secondary vein spacing is regular with little variability (<20%). The angle of the secondary veins is fairly uniform, but decreases slightly basally. In the basal section of the laminar the secondary vein angles ranges from 36 ° to 38 °, and in the middle section of the laminar vein angles range from 42 ° to 54 °. The course of the secondary veins is nearly straight, but in the lower section of the laminar the secondary vein course is curved as a result of the decurrent attachment to midvein (Figure 3.25).

Tooth morphology is known from two specimens, ACC.004-c and AM.NA.082-e, the former has teeth with a rounded apex while the latter has an acute tooth apex (Figure 3.25-a, e). This variability in tooth shape is also present in the Ardtun specimens of *Fagopsiphyllum groenlandica* (Boulter and Kvacek 1989), which indicates that this variability in tooth shape is typical of this leaf type. The other aspects of the tooth morphology of ACC.004-c and AM.NA.082-e are broadly similar, which confirms their mutual affinity.

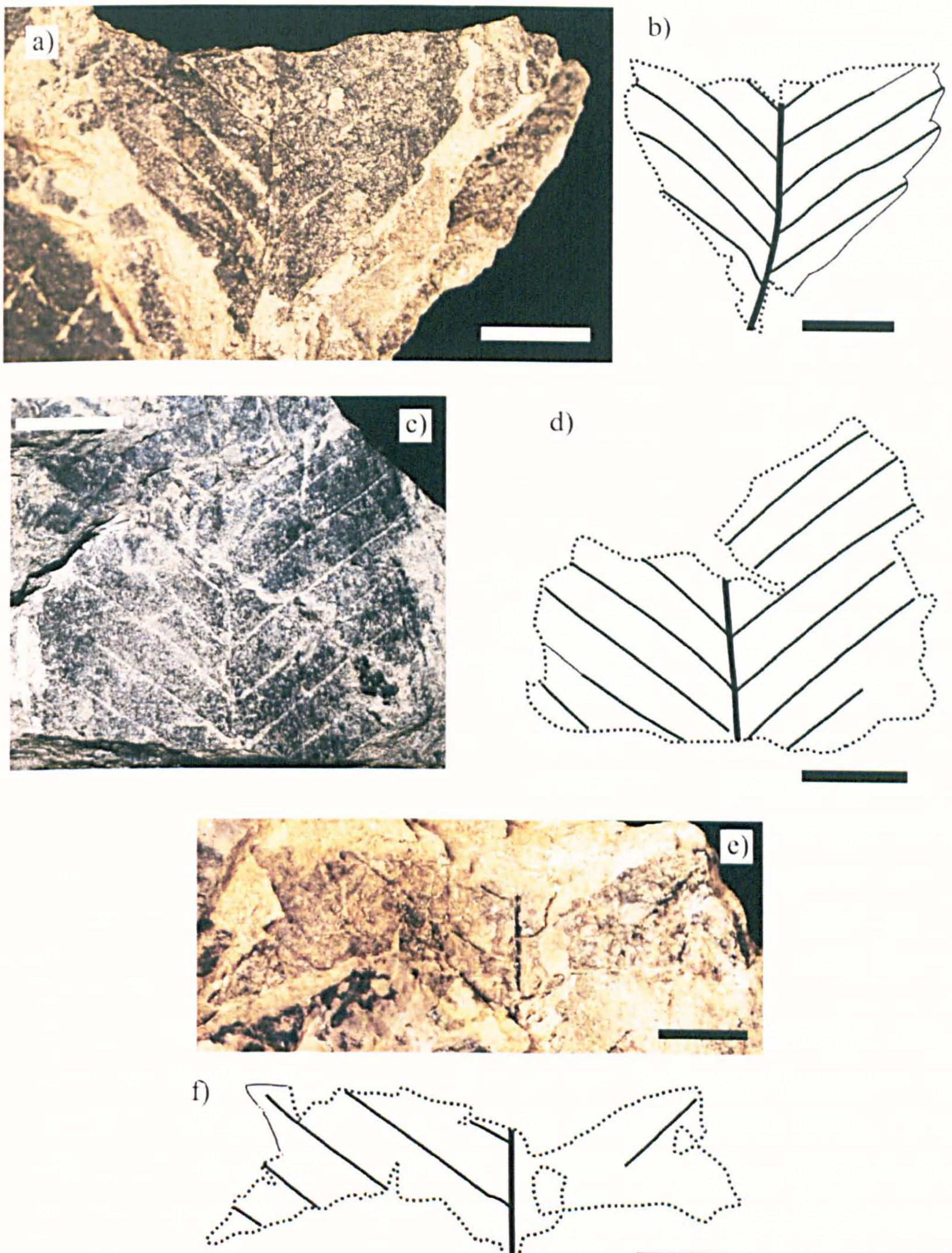

Figure 3.25. Specimens of AM5. a) ACC.004-c, b) line drawing of ACC.004-c, c) AM.NA.109-a, d) line drawing of ACC.004-c, e) AM.NA.082-e, f) line drawing of AM.NA.082-e. Scale bars = 1 cm.

3.12.5 Similarities with other fossil taxa

The distribution of the *Fagopsiphyllum* during the Paleogene indicates it was widespread, with occurrences in the North America, Greenland, Europe, Russia and Japan before it became extinct in the late Oligocene (Brown 1962, Koch 1963, Wolfe 1977, Wolfe and Wher 1987, Boulter and Kvacek 1989, Kvacek 1994, Tanai 1995).

Fossil leaves that share the same characteristic features of *Fagopsiphyllum groenlandica* have been described from the Early Paleocene of Atanikerdluk, northwest Greenland under the synonym *Quercus groenlandicus* (Koch 1963). The Greenland leaves are remarkably similar to those from the BTVP, indeed, Boulter and Kvacek (1989) reclassified the genus to *Fagopsis groenlandica* (now *Fagopsiphyllum groenlandica*) as they considered it to be the same species. The presence of *Fagopsiphyllum groenlandica* in northwest Greenland during the Early Paleocene provides further evidence that Arctic floral elements were mixing with those of Scotland, and they crossed the volcanically active land bridge of the North Atlantic Igneous Province (NAIP).

Paleogene Occurrences of *Fagopsiphyllum* are not restricted to the BTVP and the Arctic, as leaves of this type have been described from North America (Wolfe 1977, Wolfe and Wehr 1987, Manchester and Crane 1983, Postnikoff 2009). Paleocene representatives of this leaf type have been described from the Rocky Mountain region, US and Alberta, Canada. Brown (1962) described *Quercus groenlandicus* (syn *Fagopsiphyllum groenlandica?*) from the Paleocene of the Rocky Mountains, if this species is the same as *Fagopsiphyllum groenlandica* it suggests that this species had a relatively wide distribution in the Paleocene.

Fagopsiphyllum praegroenlandicum from the Early Paleocene of the Ravenscrag Formation represents another possible species of this genus (Postnikoff 2009). The specimens described in Postnikoff (2009), however, indicate that this species is markedly different to *Fagopsiphyllum groenlandica*. The secondary veins of *Fagopsiphyllum praegroenlandicum* are less uniform in angle, curvature and spacing, the teeth are more irregular in size and shape, and the Tertiary vention is markedly different to *Fagopsiphyllum groenlandica* of Ardtun, Mull. The morphology of *Fagopsiphyllum praegroenlandicum* is different to the other North American species as well, including those associated with reproductive structures (Manchester and Crane 1983). It is possible that this leaf type has been wrongly ascribed to this form genus and may represent another taxon entirely.

Fagopsiphyllum leaves have also been described from the Middle Eocene of North America from the Republic region, Washington (Wolfe and Wehr 1987). Leaves described as *Fagopsis undulata* from these localities show the same overall features of *Fagopsiphyllum*, but the teeth of *F. undulata* are more rounded and the base is more acute, and in some specimens asymmetric

(Wolfe and Wehr 1987). *Fagopsis undulata* is likely a close relative of *Fagopsiphyllum groenlandica* but it appears morphological distinct.

Fagopsis longifolia is arguably the best characterized species of this leaf type as it has been found with attached inflorescences and fruits (Manchester and Crane 1983). These attached reproductive structures demonstrate that was an extinct member of the Fagaceae; the implications of this association are discussed in greater detail in section 3.12.6. The leaves of *Fagopsis longifolia* are very similar to *Fagopsiphyllum groenlandica*, more so than the other species of *Fagopsiphyllum* described previously. The margin and secondary veins appear almost identical in most respects, the L:W ratios of the two leaf types are also consistent with ratios of 2-3:1 for both leaf types (Manchester and Crane 1983, Boulter and Kvacek 1989). The age difference between the Paleocene *Fagopsiphyllum groenlandica* and the Oligocene *Fagopsis longifolia* indicates that these two leaf types represent two distinct species, but they may be closely related.

3.12.6 Similarities with modern taxa

The discovery of *Fagopsis longifolia* leaves with attached inflorescences and fruits has provided strong evidence that leaves of this type represent members of the Fagaceae (Manchester and Crane 1983). The reproductive characteristics indicate that this plant represents an extinct member of the Fagaceae that is unlike any modern genus of this family. Manchester and Crane (1983) have suggested that this genus may have appeared in the Paleocene and that the Fagaceae were potentially beginning to diversify in the Paleocene and Early Eocene.

Manchester (1999) reclassifed the leaves of *Fagopsis* that lack any attached inflorescences to the form genus *Fagopsiphyllum*. Furthermore Manchester (1999) stated that true representatives of *Fagopsis* (those with attached inflorescences) have not been recorded outside North America. The absence of attached inflorescences with the leaves of *Fagopsiphyllum groenlandica* of Mull and Skye prevents a definitive association with the Fagaceae.

The close morphological resemblance of *Fagopsiphyllum groenlandica* and *Fagopsis longifolia* does indicate that these two leaf types may represent closely related species. On this basis the leaves of AM5 from BTVP are tentatively associated with the Fagaceae and the genus *Fagopsis*, but this association requires the discovery of inflorescences to be definitive.

3.13 Angiosperm morphotype 6 (AM6)

3.13.1 Specimen numbers

The specimen numbers of this morphotype are: ACC.001-b, g, j, AM.NA.084-h.

3.13.2 Diagnosis

Leaf attachment appears sessile. Blade attachment marginal, laminar size microphyll, laminar shape appears elliptic, blade medially symmetric, basal insertion asymmetric, unlobed, margin not preserved. Apex not preserved, base angle obtuse, base shape convex. Primary venation pinnate, naked basal veins absent, three basal veins, agrophic veins absent. Major secondary veins semicraspedodromous, interior secondary veins absent, minor secondary veins absent, major secondary vein spacing irregular, secondary vein angle increasing proximally, major secondary attachment excurrent. Intersecondary span > 50% of subjacent secondary veins, occur one per intercostal area, proximal course parallel to major secondary, and distal course basiflexed or parallel to major secondary. Intercostal tertiary veins irregular reticulate. Epimedial tertiary veins reticulate with proximal course parallel to intersecondary and distal course parallel to intercostal tertiary veins. Exterior tertiary course looped. Quaternary vein fabric alternate percurrent. Quinternary vein fabric reticulate. Aerolation development moderate, freely ending veinlets absent. Marginal venation looped.

3.13.3 Identification

Angiosperm morphotype 6 (AM6) is a rare component of the Allt Mor leaf assemblage with only four specimens that are considered to belong to this morphotype, three of which occur on the same laminar of one sample (ACC.001). These specimens do not have their apex or margin preserved (except proximally on ACC.001-g) but have very clear venation clarity, which has facilitated the identification of this morphotype.

One leaf type of Ardtun, Mull, *Juglandiphyllites ardtunensis*, closely resembles AM6 in both its venation pattern and basal morphology (Boulter and Kvacek 1989). The base shape of AM6 is convex with an asymmetric basal insertion of ~2 mm which is identical to *Juglandiphyllites ardtunensis*. The base of AM6 appears to lack a petiole, which may suggest the leaves had a sessile attachment, which seems to be the case for *Juglandiphyllites ardtunensis* (Boulter and Kvacek 1989). Both leaf types also have similar basal margin characteristics, which are entire and slightly erose.

Venation patterns of both leaf types are broadly similar with pinnate, semicraspedodromous primary and secondary veins, an absence of agrophics, irregular reticulate intercostal and epimedial tertiary veins, irregular reticulate quaternaries and reticulate quinternary veins. One difference has been observed in their venation characteristics, however, and that is the frequency and strength of the intersecondary veins. The intersecondary veins of AM6 are numerous, with typically one per intercostal area. The best preserved specimen of *Juglandiphyllites ardtunensis* (V25133) has only one intersecondary vein present. This intersecondary is present in the upper portion of the laminar and has a course that is similar to some of the intersecondary veins of AM6.

The similarity in all vein orders and basal morphology indicates that these two leaf types may represent the same or closely related taxa. The only visible difference between the two leaf types is their intersecondary vein morphology. Whether the frequency of the intersecondary veins represents intra-specific variation or inter-specific differences is currently unclear because of the low number of specimens of both AM6 and *Juglandiphyllites ardtunensis*.

It is likely that these leaf types are closely related, but whether they represent the same species is unclear. AM6 is therefore regarded as being in the same form genus as *Juglandiphyllites ardtunensis* but as a different species until further morphological evidence can be found that could unite the two leaf types. AM6 is therefore considered to be *Juglandiphyllites* sp.1.

3.13.4 Discussion

Specimens of AM6, although limited in number, have provided a good understanding of its overall form and venation characteristics (Figures 3.26 and 3.27). The original laminar area and size class of AM6 is difficult to determine due to the limited number of specimens and their fragmented preservation. Two of the specimens of AM6 are relatively complete, ACC.001-b and AM.NA.084-h (Figure 3.26-a and 3.27-a), which have laminar areas (fragmented perimeter) of 1849 mm^2 and 1536 mm^2 respectively. This indicates that the leaves were originally microphyll to notophyll prior to their fragmentation. The lack of margin preservation prevents a reliable determination of the shape of the leaf, but the venation near to where the margin would be in ACC.001-b and the curvature of its secondary veins indicate that its shape is elliptic.

The base of AM6 is completely preserved in one specimen, ACC.001-g (Figure 3.26-c), which shows that that this leaf type had a convex base shape with an asymmetric basal insertion. The presence of an asymmetric basal insertion and apparent lack of petiole indicates that this leaf type may have had a sessile attachment, and possibly therefore the leaflets may have a compound arrangement. The base angle of ACC.001-g is ~95 °, which indicates that the basal angle is obtuse but close to being acute. Margin is preserved around the base of ACC.001-g and is entire and slightly erose (Figure 3.26-c). It is unclear whether the rest of the margin was entire, comparisons with *Juglandiphyllites ardtunensis* of Ardtun suggests that the margin of AM6 may have possessed a limited number of small crenate teeth. Additional specimens of

AM6 are required to confirm whether the margin was entire or toothed, which could help determine if this morphotype is the same species as *Juglandiphyllites ardtunensis*.

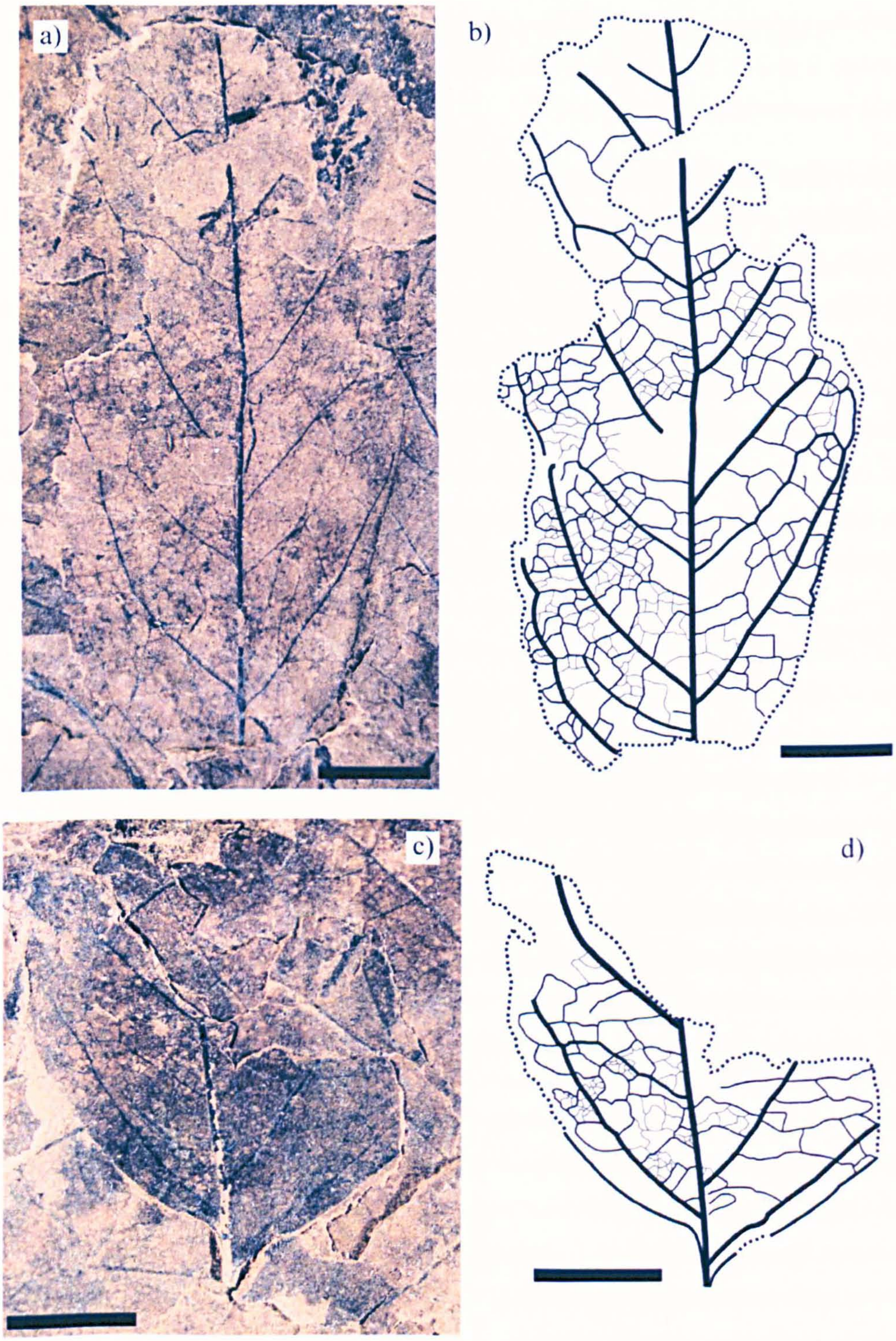

Figure 3.26. Specimens of AM6. a) ACC.001-b, b) line drawing of ACC.001-b, c) ACC.001-g, d) line drawing of ACC.001-g. Scale bars = 1 cm.

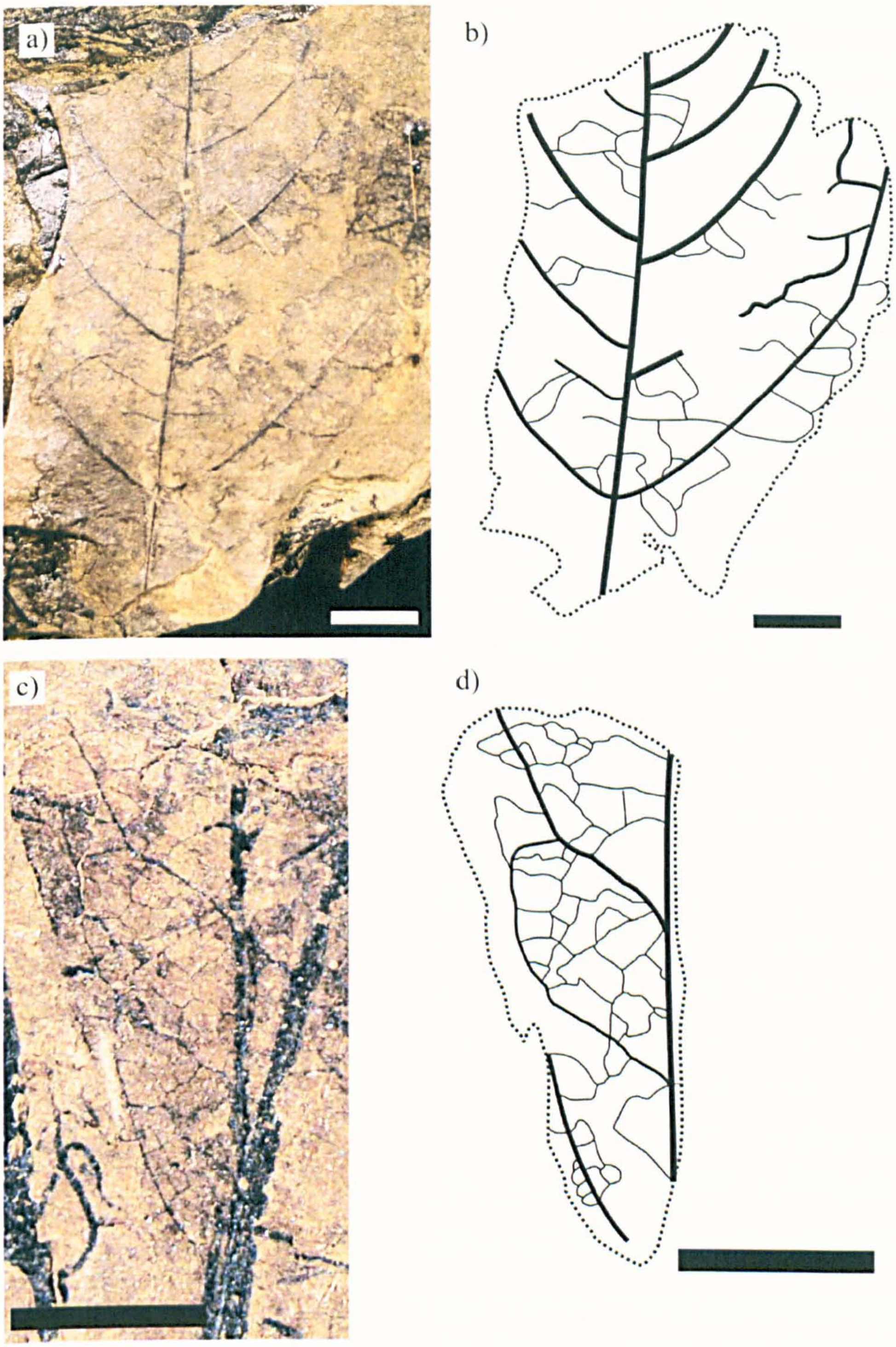

Figure 3.27. Specimens of AM6. a) AM.NA.084-h, b) line drawing of AM.NA.084-h, c) ACC.001-j, d) line drawing of ACC.001-j. Scale bars = 1 cm.

The venation patterns of this morphotype are well preserved in three specimens, ACC.001-b, g and j (Figure 3.26-a, c and 3.27-c). Secondary vein spacing appears irregular on the most complete specimen (ACC.001-b), the cause of this irregular spacing may be related to the presence of the intersecondary veins. The intersecondary veins diverge from the laminar at irregular intervals, and may function in a similar way to the major secondary veins (contributing to their irregular spacing). Major secondary vein angles appear be relatively uniform with angles in the central to upper portion of the laminar ranging from 34 ° to 47 ° (mean 40 °). ACC.001-g shows there is slight increase basally, with secondary vein angles of 40 ° to 59 °.

The intersecondary veins of this morphotype are one of its diagnostic features and were used to establish its identity. The proximal course of the intersecondary veins appears not to vary and is parallel to the major secondary vein. The distal course of the intersecondary veins is more variable and can be basiflexed or parallel to the major secondary.

The intercostal tertiary veins are irregular reticulate and form variable polygonal vein shapes, the epimedial tertiaries are reticulate with a proximal course parallel to intersecondary and a distal course parallel to the intercostal tertiaries. The marginal tertiaries form a series of small loops between the leaf margin and the outer edge of the secondary veins. The irregular reticulate quaternary and reticulate quinternary veins, along with the lower order venation form areoles of a fairly consistent size and shape indicating the areolation development is moderate to good. Freely ending veinlets appear absent, but venation of this high order is only preserved in limited areas of one specimen (e.g. ACC.001-g).

3.13.5 Similarities to other fossil taxa

The leaf form and venation characteristics of AM6 indicate it represents a member of the form genus *Juglandiphyllites*, which is associated with the family Juglandaceae. This form genus represents a useful if somewhat ambiguous taxon, with leaves that show affinities to the Juglandaceae but cannot confidently associated with a specific genus within this family (Manchester 1989).

The fossil record of the Juglandaceae is extensive. Leaves, wood, pollen, and reproductive structures are known from across the Northern Hemisphere from the Cretaceous and Paleogene (Manchester 1989). The extensive review of the early history of the Juglandaceae by Manchester (1989) indicates that many modern genera including *Platycarya*, *Cyclocarya*, *Pterocarya* and *Juglans* as well several extinct genera had evolved in the Paleogene.

Two species of *Juglandiphyllites* are present in the Ardtun leaf assemblage of Mull: *Juglandiphyllites ardtunensis* and *Juglandiphyllites finlayii* (Boulter and Kvacek 1989). As discussed in section 3.13.3 *Juglandiphyllites ardtunensis* may represent a closely related species to AM6, while the morphology of *Juglandiphyllites finlayii* is markedly different. *Juglandiphyllites finlayii* has a serrate margin with up two tooth orders, semicraspedodromous to craspedodromous secondary veins and weaker intersecondary veins that set it apart from AM6.

Two species of juglandaceous affinity have been recognised from the Late Paleocene Cold Ash Quarry of the Reading Beds, southern England (Crane and Manchester 1982). One of these leaflets shows similarities to modern genus *Pterocarya* while the other although similar, is regarded to represent an extinct genus (Crane and Manchester 1982). These two leaf types are distinctly different to the leaves of AM6, their margins are finely serrate, and they lack the characteristic intersecondary veins and reticulate intercostal tertiary veins of AM6.

Leaves associated with the Juglandaceae are present in the Early Paleocene of Greenland (*Juglandiphyllum denticulatum*, Koch 1963). The base shape of *J. denticulatum* is straight with an acute angle and its margin is finely serrate (Koch 1963), these features show that it is distinct from AM6.

Fossil leaves of *Juglandiphyllites glabra* from the Paleocene of Wyoming and Montana are exceptionally well preserved (Manchester and Dilcher 1997). This North American species has specimens that have their leaflets attached to a rachis, which indicates that the leaves were compound, with one terminal leaflet and five to seven lateral leaflets (Manchester and Dilcher 1997). This leaflet arrangement is characteristic of the Juglandaceae, which is partially confirmed by the association of *Polyptera* fruits with the leaves. The leaves of AM6 are dissimilar to *Juglandiphyllites glabra*, which itself displays a resemblance to *Juglandiphyllum denticulatum* of Greenland. Leaves associated to the Juglandaceae have been reported from other North American Paleogene localities (Brown 1962, Wolfe 1966, Hickey 1977, Wolfe 1977, Crane et al. 1990, Manchester and Dilcher 1997). All specimens of these juglandaceous leaf types have morphological characteristics that set them apart from AM6.

The absence of juglandaceous leaf types similar to AM6 and *Juglandiphyllites ardtunensis* of Mull from other Northern Hemisphere regions may indicate that these plants were endemic to the BTVP.

3.13.6 Similarities to modern taxa

Boulter and Kvacek (1989) discussed the affinities of *Juglandiphyllites ardtunesis* and stated their reticence in assigning this taxon to a modern group within the Juglandaceae. *Juglandiphyllites ardtunesis* and AM6 does share the same basic venation morphology of modern members of the Juglandaceae, as well the asymmetric basal insertion and apparent absence of a petiole (Manchester 1989). The Juglandaceae appear to have evolved in Late

Cretaceous or Paleocene, but relatively few modern genera have been identified in the Paleocene (Manchester 1989). It is unclear to which modern or extinct genus the Mull and Skye forms most resemble.

The marginal characters of *Juglandiphyllites ardtunesis* are more indicative of *Juglans* but this association is tentative at best. In terms of gross morphology the leaves of the extant *Juglans* look remarkably like those of *Juglandiphyllites ardtunesis* and AM6. The modern leaves do, however, differ from fossil forms in their tertiary venation. The modern leaves have mixed percurrent intercostal tertiary veins that are unlike the reticulate tertiary veins of the Paleocene BTVP forms.

Juglandaceous pollen is present in the interbasaltic sequences of the BTVP, and is both relatively common and diverse (Boulter and Kvacek 1989, Jolley 1997, Jolley et al. 2009). The presence of pollen attributed to the Juglandaceae suggests that this family was present in the BTVP during the Paleocene, and provides further support that AM6 may be a member of the Juglandaceae. Pollen genera found in the BTVP sequences include *Caryapollenites*, *Momipites*, *Platycaryapollenites*, and *Plicapolis* (Jolley et al. 1997, Jolley et al. 2009). The diversity of juglandaceous pollen types suggests that juglandaceous plants were potentially diverse components of BTVP plant communities. Possible producers of the pollen include members of the sub-tribe Caryinae (*Caryapollenites*), basal members of the Engelhardioideae tribe (*Momipites*) and extinct forms of Platycaryeae sub-tribe (*Platycaryapollenites)* (Manchester 1989). Modern members of these sub-tribes have leaves that are unlike those of AM6, but this may be due to the relatively undifferentiated nature of Paleocene pollen attributed to the Juglandaceae (Manchester 1989).

The absence of Juglandaceae reproductive structures from the Skye and Mull assemblages prevents an accurate assignment to this family. The distinctive leaf morphology of AM6 and presence of juglandaceous pollen does suggest it was probably a member of this family. On this basis AM6 is tentatively attributed to the Juglandaceae, but its generic affinity are unknown.

3.14. Angiosperm morphotype 7 (AM 7)

3.14.1 Specimen numbers

The specimen number of this morphotype is: NMS.G.2004.29.008-e.

3.14.2 Diagnosis

Laminar size nanophyll, laminar L:W unknown, laminar shape appears elliptic, blade appears medially symmetric, base symmetry unknown, unlobed, margin serrate. Apex not preserved, base angle appears acute, base shape unclear (appears convex or straight). Primary venation pinnate, number of basal veins unknown, agrophic veins absent. Major secondary veins semicraspedodromous, interior veins absent, minor secondary veins absent, major secondary vein spacing decreasing proximally, secondary vein angle smoothly increasing proximally, major secondary attachment excurrent. Intersecondary length <50% of subjacent secondary, proximal course parallel to major secondary, distal course parallel to subjacent major secondary, vein frequency ~1 per intercostal area. Intercostal tertiary vein fabric unclear (appears percurrent with an acute angle), angle variability unknown. Epimedial tertiary veins opposite percurrent with a proximal course acute to midvein and distal course parallel to intercostal tertiary veins. Exterior tertiary course not visible. Higher order venation not visible. Tooth spacing irregular with two orders of teeth, and 3 teeth/cm. Sinus shape angular, tooth shape concave/convex. Principal vein present with termination at apex of tooth. Tooth apex appears mucronate.

3.14.3 Identification

Angiosperm morphotype 7 (AM7) is represented by a single fragmented specimen (NMS.G.2004.29.008-a), but has enough morphological characteristics preserved to distinguish it from other angiosperm morphotypes from Skye. This morphotype has distinctive secondary and tertiary vein patterns, marginal characteristics.

The shape, venation and marginal characteristics indicate that AM7 may be similar to *Juglandiphyllites finlayii* of Ardtun, Mull (Boulter and Kvacek 1989). The single specimen of AM7 although fragmented appears to have a similar shape to this taxon, which appears elliptic, relatively long and narrow (L:W ~3:1) and has appears to have an acute base angle.

The major secondary veins of *Juglandiphyllites finlayii* are semicraspedodromous in the proximal portion of the laminar, which appears similar to AM7. Boulter and Kvacek (1989) note that one of the characteristic features of *Juglandiphyllites finlayii* is the asymmetry of its major secondary vein angles. The secondary veins on one side of the laminar are curved and relatively acute, while those on the other side have straighter courses and are obtuse to the midvein. This is apparant for AM7, but it is unclear if this pattern continues further up the laminar. *Juglandiphyllites finlayii* also has intersecondary veins that appear similar to AM7. As they span <50% of the subjacent major secondary and have proximal and distal courses that are parallel to the major secondary veins.

The margin of *Juglandiphyllites finlayii* is serrate with prominent teeth like AM6 but differs to this morphotype in that it has two teeth orders, which Boulter and Kvacek (1989) described as "coarsely double dentate". This feature is not apparent in AM7, but may be due to the limited number of teeth preserved. The teeth of AM7 have concave distal and convex proximal flanks and the tooth apex is nearly parallel to the midvein. The teeth of *Juglandiphyllites finlayii* have convex/convex shapes and the tooth apex is more obtuse relative to the midvein. The tooth apex of AM7 appears to have an opaque projection, which suggests it may be mucronate. The tooth apex of *Juglandiphyllites finlayii* appears simple and lacks any discernable projection.

The shared characteristics between AM7 and *Juglandiphyllites finlayii* indicate that these two leaf types may be related, but significant differences in their margins shows they represent different species. AM7 also shares two features in common with AM6 (*Juglandiphyllites* sp.1) as well, which include the presence of intersecondary veins and the course of the most basal secondary veins. The basal most proximal vein course of AM6 appears to run along close to the margin before they join the superjacent secondary vein close to the margin.

The similarity of AM7 with two species of *Juglandiphyllites* indicates that it may be assignable to this form genus, but as a new species. Additional specimens of this morphotype are required to provide further evidence of its identity but based on its morphological characteristics its assignment to the form genus *Juglandiphyllites* appears justified. AM7 is therefore regarded as *Juglandiphyllites* sp.2.

3.14.4 Discussion

The single specimen of AM7, NMS.G.2004.29.008 (Figure 3.28) appears to be unique to the Allt Mor assemblage because of its small laminar size. The fragmented area of NMS.G.2004.29.008-a, is 80 mm^2, estimates of its original size based on the curvature of the laminar indicate it may have been have been little more than 150 mm^2. This morphotype is the only one in the Skye assemblages that appears to have a nanophyll leaf size, while the other angiosperm morphotypes appear to be least microphyll.

The base of AM7 is not preserved so it is difficult to determine its original shape, but the curvature of the margin preserved in the proximal portion of the laminar indicates that the shape may have been convex or straight. The angle of the base is equally difficult to determine but appears to be acute with an angle of ~70°.

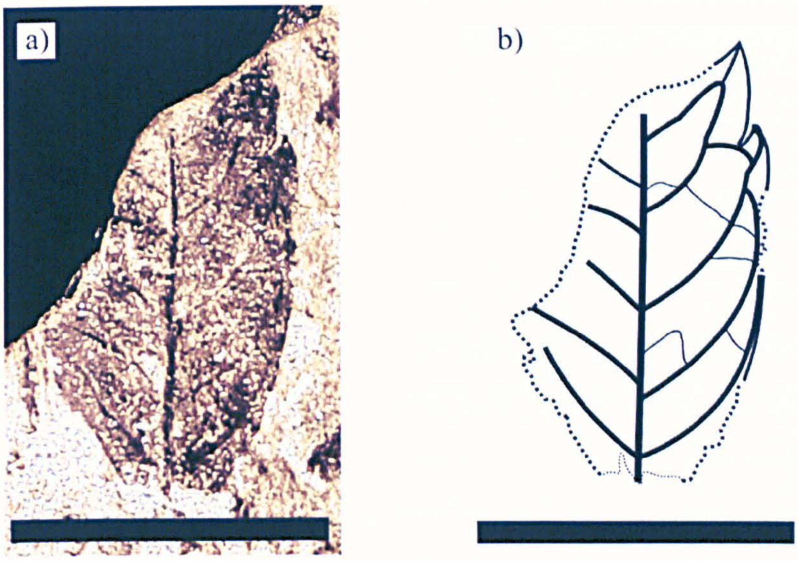

Figure 3.28. The single specimen of AM7. a) NMS.G.2004.29-008-a, b) line drawing of NMS.G.2004.29-008-a. Scale bars = 1 cm.

The major secondary veins are simple semicraspedodromous and only form one loop between the secondary veins before they branch off towards the margin and become principal veins for the teeth. The major secondary vein angles vary on either side of the laminar, those preserved on the right side of the laminar are curved and have more acute vein angles, those on the left have a straighter course and have more obtuse angles (Figure 3.29).

The tertiary venation is poorly preserved for this morphotype but appears to be opposite percurrent, the course of which varies from convex to straight. The variability of the intercostal secondary veins is unclear due to the limited number preserved but they appear to be obtuse. The epimedial secondary veins proximal course is acute to the midvein and its distal course is parallel to the intercostal tertiary veins.

The marginal characteristics of AM7 are very distinctive because of the tooth shape and the orientation and features of the tooth apex. The distal flanks of the teeth are concave and the proximal flanks are concave with a relatively deep, angular tooth sinus (Figure 3.29). The teeth appear almost hook like with the distal flank curving sharply inwards, causing the apex of the tooth to be close to the margin and pointing almost parallel with that of the midvein. A principle vein is present and enters the centre of the tooth and curves distally along the margin before terminating at the tooth apex. The most completely preserved tooth of AM7 has an apex that forms a vascularised opaque mass indicating it may be mucronate (Figure 3.29).

3.14.5 Similarities to other fossil and modern taxa

This morphotype was identified as a new species, *Juglandiphyllites* sp.2. Its morphology and those of the other members of this form genus indicate that it is a member of the Juglandaceae whose generic affinity is uncertain. Comparisons with the fossil relatives of AM6 (*Juglandiphyllites* sp.1.) discussed in section 3.13.5 indicate that this morphotype is unlike other Paleocene members of the Juglandaceae from the Northern Hemisphere. These Paleocene members of the Juglandaceae discussed in section 3.13.5 are also different morphologically to AM7, which suggests that this morphotype, like AM6, may be endemic to the BTVP.

AM7 appears to be similar to *Juglandiphyllites finlayii* of Ardtun, Mull but was shown to be a distinct species (see section 3.14.3). Boulter and Kvacek (1989) commented on the taxonomic affinity of *Juglandiphyllites finlayii* and suggested tentatively that this leaf type may be related to the modern genus *Platycarya* of the Juglandaceae. *Platycarya*-like pollen is known from the BTVP (*Platycaryapollenites*) (Jolley 1997, Jolley et al. 2009), which suggests *Platycarya*-like pollen producers were present in the BTVP. AM7, and possibly *Juglandiphyllites finlayii* do not appear to be that similar to modern or Paleogene representatives of the *Platycarya* (Wing and Hickey 1984, Atkinson and Upson 2006). Another morphotype from the Allt Mor assemblage, AM8 (see section 8.15) appears to resemble this genus more, which suggests AM7 may represent another juglandaceous genus entirely.

The leaf morphology of *Juglandiphyllites finlayii* and AM7 appears to be similar to modern *Alafaroa* of the Juglandaceae (Dilcher and Manchester 1986). The margin of AM7 in particular, is remarkably similar to modern species of *Alafaroa* (*A. costaricaensis* and *A. costaricaensis* spp.) figured in Dilcher and Manchester (1986) in both shape and the tooth apex form. The tooth apex of both AM7 and modern *Alafaroa* appears to have an opaque structure at the tooth apex and the shapes are both concave/convex. These features along with a broadly similarity in venation patterns may indicate that AM7 is related to *Alafaroa.*

The genus *Alafaroa* is part of the Engelhardioideae tribe, which includes three other modern genera; *Engelhardia*, *Oremunnea*, and *Alfaropsis* (Manos and Stone 2001, Manos et al. 2007). Fossil and molecular evidence of this tribe indicates they have shared ancestry, and first appeared in the Paleocene (Manchester 1989, Manos and Stone 2001, Manos et al. 2007). Fruits of *Casholdia microptera* from the Late Paleocene Cold Ash Quarry of the Reading Beds in southern England, may represent one of the oldest records of the Engelhardioideae tribe (Crane and Manchester 1982, Manchester 1989, Manos and Stone 2001, Manos et al. 2007). The morphology of the winged fruits of *Casholdia microptera* indicates that it was possibly an early ancestor of the Engelhardioideae tribe that is distinct from the modern genera in this tribe. Similar fruits are also present from the mid Paleocene of Menat, France (Manchester 1989), which suggests that early members of this tribe were common in Europe during the Paleocene.

Casholdia-like fruits have not been identified in any of the BTVP floral assemblages, but pollen attributed to the Engelhardioideae tribe is present (*Momipites*-type) (Jolley 1997, Jolley et al. 2009). Dispersed anthers of juglandacous affinity were found in association with *Casholdia* in the Cold Ash Quarry site, and the pollen extracted from these anthers was identified as *Momipites* (Crane and Manchester 1982). *Momipites*-type pollen is produced by modern members of the Engelhardioideae tribe and the presence of this pollen type from the Cold Ash Quarry and the BTVP provides further evidence that this tribe was present in Europe during the Paleocene.

Four species of *Momipites* pollen are present within sedimentary sequences of the BTVP (Jolley 1997, Jolley et al. 2009). The diversity and distribution of this pollen type indicates that *Momipites*-pollen producers were a common component of the BTVP flora. The association of *Momipites* with other members of the Engelhardioideae tribe is not unequivocal, however, as it has been found in association with other genera of the Juglandaceae in North America (Manchester 1989). In Europe, however, *Momipites* pollen has only been associated with the fruits of the Engelhardioideae tribe (Manchester 1989). This indicates that *Momipites* pollen, AM7, and possibly *Juglandiphyllites finlayii* may represent archaic members of the Engelhardioideae tribe. The association with this tribe is not definitive as *Casholdia*-like fruits, and leaves with cuticle preserved have yet to be discovered in the BTVP plant assemblages that could confirm this assertion. AM7 is therefore tentatively associated to the Engelhardioideae tribe until its relationship can be more conclusively determined.

3.15 Angiosperm morphotype 8 (AM8)

3.15.1 Specimen numbers

The specimen numbers of this morphotype are: AM.NA.023, 111-b, 184, AM.NA.2008: 006-a, 008-a, 010-a, 011-c, NMS.G.2004.29: 008-f, 011-c, 014-c, 023-f, i, l, 055-e, f, 066-a, 066-b, c, j, 072-a, ACC.AM.099-b, NMSG.2002.64: 5-a, b, c, d.

3.15.2 Diagnosis

Leaf attachment appears sessile, leaf organisation unclear (possibly pinnately compound), leaflet attachment sessile. Blade attachment marginal, laminar size microphyll to notophyll, laminar L:W ratio ~2.8:1 to >5:1, laminar shape elliptic. Blade medially symmetrical or with an asymmetric basal insertion, unlobed, margin serrate. Apex angle acute, apex shape acute or acuminate with a drip-tip, base angle acute to slightly obtuse, base shape convex. Primary venation pinnate, naked basal veins absent, one basal vein present, agrophic veins absent. Major secondary veins craspedodromous, interior secondary veins absent, minor secondary veins craspedodromous, major secondary vein spacing decreasing proximally, secondary angle inconsistent, regular or smoothly decreasing proximally, major secondary attachment excurrent.

Intersecondary length > 50% of subjacent major secondary, proximal course parallel to major secondary, distal course parallel to major secondary, vein frequency < 1 per intercostal area. Intercostal tertiary vein fabric opposite percurrent with obtuse vein angle. Epimedial tertiary veins opposite percurrent with proximal course perpendicular to midvein or parallel to the midvein and distal course parallel to intercostals tertiary veins. Exterior tertiary not preserved. Higher order venation not visible. Tooth spacing regular to irregular, two orders of teeth, and ~2 teeth per/cm. Sinus shape angular or rounded, tooth shapes straight/straight, flexous/straight or convex/straight. Principal vein present with termination at the tooth apex. Tooth apex appears simple.

3.15.3 Identification

Angiosperm morphotype 8 (AM8) is one of the more abundant leaf types of the Allt Mor assemblage of Skye and has many well preserved specimens, that have aided its identification. The venation and marginal characteristics of AM8 appear broadly similar to AM7 and *Juglandiphyllites finlayii* of Ardtun, Mull. Of these two leaf types, *Juglandiphyllites finlayii* appears most similar to AM8 but can be distinguished from this species by its margin morphology. The teeth of AM8 are primarily simple, they have straight/straight, flexous/straight or convex/straight tooth shapes compared to the more convex/convex compound teeth of *Juglandiphyllites finlayii*. The teeth of AM8 although serrate like *Juglandiphyllites finlayii* are more perpendicular to the trend of the margin (near dentate) compared to those of the Mull leaf type whose teeth follow the trend of the margin. These features, and the simple tooth apex of AM8 differentiates it from AM7.

Despite of these differences in leaf form AM8 does appear to be related to these aforementioned leaf types, as its secondary veins have a similar curved course and the intersecondary veins appear broadly similar. This suggests that AM8 may represent another species of *Juglandiphyllites*. One feature in particular provides additional evidence that AM8 is a member of the Juglandaceae and that is its leaf attachment. Sample NMS.G.2004.29.66 has what appear to be three leaflets of AM8 attached to a rachis-like structure. This arrangement is typical of the Juglandaceae and has been observed in other Paleocene forms of this family (Manchester 1989, Manchester and Dilcher 1997).

The leaf form of AM8 appears most similar to modern *Platycarya strobilacea* in its overall shape, apex and basal form, including attachment, margin and venation characteristics (Atkinson and Upson 2006). *Platycarya*-like pollen is present in BTVP including some of the Skye sequences (Jolley 1997), which are among the oldest records of this pollen type (Manchester 1989), this suggests that AM8 may represent an ancestral species of *Platycarya*.

The absence of *Platycarya*-like reproductive structures in the BTVP prevents a definitive association with this genus, however. It is likely that this morphotype represents a species of *Platycarya*, or species that is ancestral to this genus, it is therefore regarded as "*Platycarya* cf." until its relationship with modern and extinct representatives of *Platycarya* can be more adequately determined.

3.15.4 Discussion

The morphology of AM8 is well understood as number of specimens are well preserved (e.g. AM.NA.184-a, NMS.G.2004.29.11-c, NMS.G.2004.29.066-b, NMSG.2002.64.5-a, AM.NA.2008.009-a, AM.NA.023-a) (Figures 3.29 to 3.31). This morphotype appears to be unique among the angiosperm morphotypes of Skye as its leaflet attachment is partially preserved. Three leaflets of AM8 (NMS.G.2004.29.066-b, h, i) appear to be attached to a rachis-like structure (Figure 3.29). The arrangement and orientation of these leaves is consistent with the curvature of a plant organ that appears similar to a rachis (Figure 3.29-a). The bases of these specimens terminate at, or near the edge of the rachis. One leaflet (NMS.G.2004.29.066-b) appears to have an organic connection with the rachis-like structure, the primary vein at its most basal point gently curves towards the rachis and appears attached at this point (Figure 3.29-a, c). The leaflets appear to lack a true petiole, and none of the disarticulated specimens in the Allt Mor collection have a petioles preserved (Figures 3.29-c, 3.20-a, c). This arrangement suggests that the leaflets had a sessile attachment to the rachis and may have been pinnatley compound.

The terminal leaflet of this arrangement, if originally present, is not preserved. A disarticulated specimen (NMS.G.2004.29.011-c) may potentially represent a terminal leaflet (Figure 3.30-c). It is one of the largest specimens of AM8 and appears to be longer and narrower than other specimens of this morphotype (L:W ratio ~5:1), but in venation and margin characteristics it is the same. If this specimen does represent a terminal leaflet, it may suggest that the leaflets had a variable form depending on their position on the rachis. The base of some specimens have been preserved (e.g. Figures 3.29-c, 3.20-a, c) and show that AM8 had an asymmetric basal insertion, a feature it shares with AM6. This feature is common in leaves that have a sessile attachment, such as those in the Juglandaceae (Manchester 1989); this suggests that AM6 may have also been attached to a rachis.

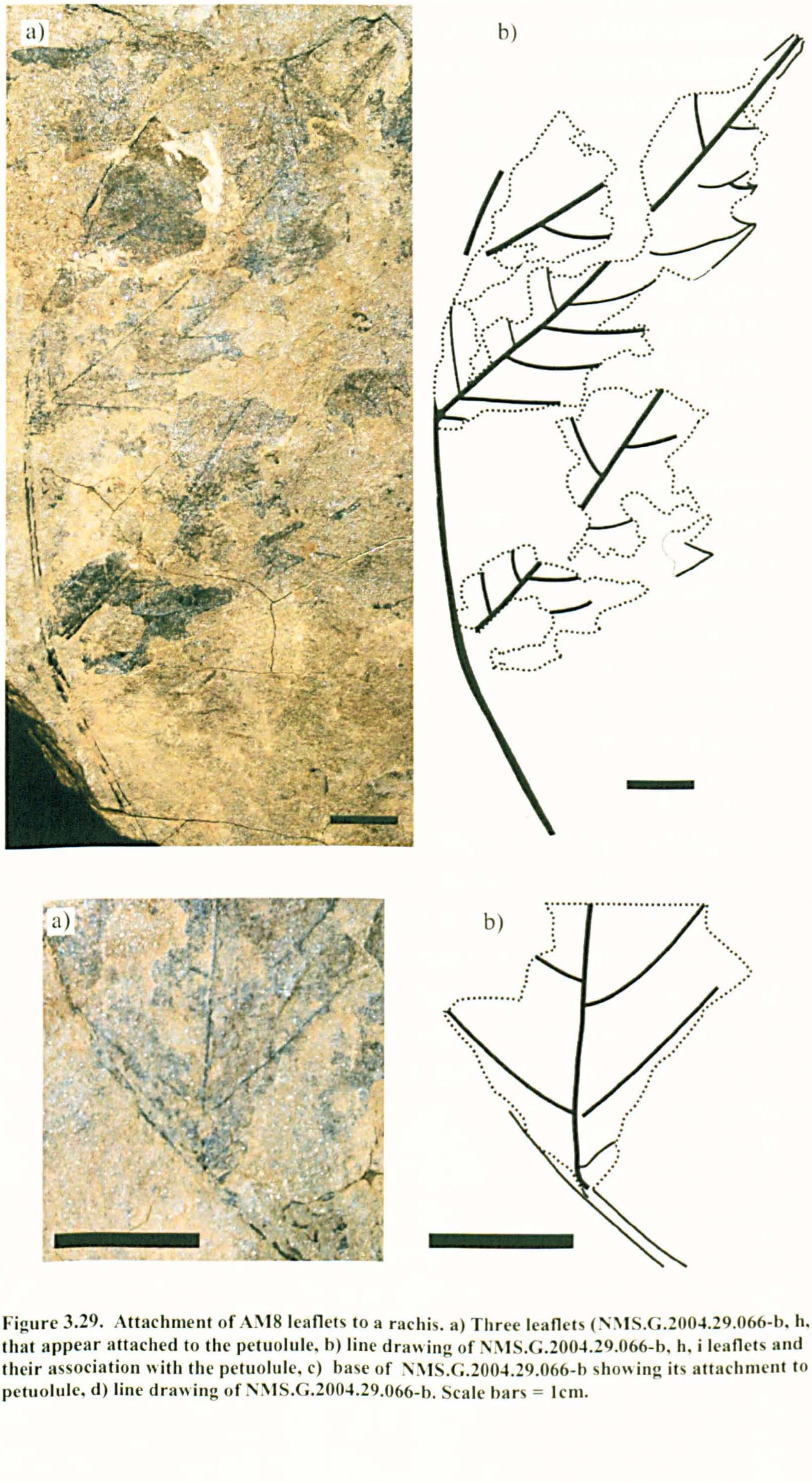

Figure 3.29. Attachment of AM8 leaflets to a rachis. a) Three leaflets (NMS.G.2004.29.066-b, h, i) that appear attached to the petuolule, b) line drawing of NMS.G.2004.29.066-b, h, i leaflets and their association with the petuolule, c) base of NMS.G.2004.29.066-b showing its attachment to the petuolule, d) line drawing of NMS.G.2004.29.066-b. Scale bars = 1cm.

Figure 3.30. Examples of well preserved specimens of AM8. a) AM.NA.184-a, b) line drawing of AM.NA.184-a, c) NMS.G.2004.29.11-c, d) line drawing of NMS.G.2004.29.11-c, e) NMS.G.2004.29.066-b, f) line drawing of NMS.G.2004.29.066-b, g) NMSG.2002.64.5-a, h) line drawing of NMSG.2002.64.5-a. Scale bars = 1 cm.

Determining the size range of this morphotype is more reliable than other more fragmented morphotypes of Skye as several specimens are nearly complete, or complete enough to reliably determine their size class (e.g. AM.NA.0184-a, NMS.G.2004.29.011-c, NMS.G.2004.29.066-b, AM.NA.2008.009-a) (Figures 3.30-a, c, e and 3.31-a). These specimens have laminar areas that range from 1213 mm^2 to 2466 mm^2, which indicates that the leaves of AM8 were microphyll to notophyll. Length:width ratio can be reliably determined for at least two specimens

(AM.NA.0184-a, NMS.G.2004.29.066-b) and approximated for a third (NMS.G.2004.29.011-c) (Figure 3.30-a, c, e). Specimens NMS.G.2004.29.066-b and AM.NA.0184-a have length:width ratios of ~2.5:1 and ~2.8:1 respectively and as discussed previously NMS.G.2004.29.011-c has significantly different L:W ratio of ~5:1.

Apex angle is acute, two specimens (NMS.G.2002.64.5 and AM.NA.0184-a) have apexes of ~22.2 ° and~29 °, while NMS.G.2004.29.066-b has an apex angle of ~69 °. Apex shape is variable it can be either acuminate with a distinct drip-tip (e.g. NMS.G.2002.64.5-a, NMS.G.2004.29.066-b, j) or straight (e.g. AM.NA.0184-a) (Figure 3.30-a, c, g). Base shape is convex with an asymmetric basal insertion. Base angle is variable and can be acute with an angle of 82 ° (NMS.G.2004.29.011-c) to obtuse ~103° (AM.NA.0184-a) (3.30-a, c).

The course of AM8 craspedodromous major secondary veins are often strongly curved, this feature in conjunction with the presence of intersecondary veins was used to assign some of the more fragmented specimens to this morphotype. Major secondary vein spacing in the central portion of the laminar is fairly irregular, but categorically AM8 spacing is regarded to decrease proximally.

Major secondary angle vein is variable, some specimens (e.g. NMS.G.2004.29.049-h, AM.08.L4.01-a) appear to have inconsistent vein angles across the course the laminar, while others s have veins whose angles either increase proximally (NMS.G.2004.29.023-I, NMS.G.29.084-a, AM.NA.023-a), or decrease proximally (e.g. NMS.G.2004.29.011-c). The angles of the secondary veins in the central portion range from 49 ° to 82 ° but are typically between 50 ° to 70 °. The angle of the secondary veins appears to be strongly influenced by the degree to which the secondaries veins curve; the relatively straighter veins have more acute angles, while the curved veins are more obtuse.

Intersecondary vein frequency is difficult to determine for AM8 as they are often poorly preserved because they are a lower gauge than the major secondary veins. Specimens that have higher venation clarity appear to have relatively few of them, with less than one per intercostal area. The length of the intersecondary veins are relatively short and none observed are longer than 50% of subjacent major secondary veins. The proximal course of the intersecondary veins is typically perpendicular to the midvein, but some are parallel to the major secondaries, the distal course is parallel to the major secondary veins.

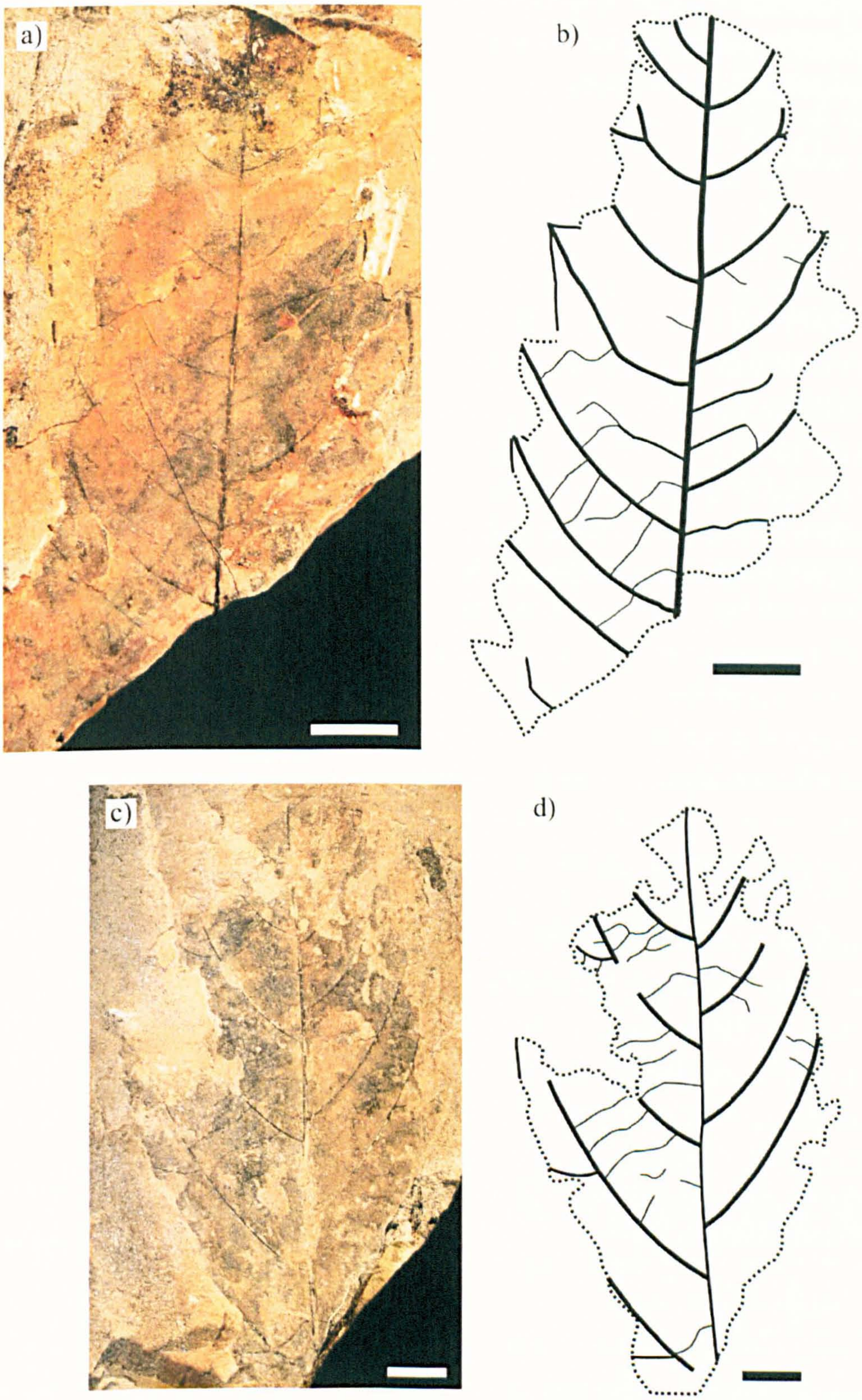

Figure 3.31. Examples of well preserved specimens of AM8. a) AM.NA.2008.009-a, b) line drawing of AM.NA.2008.009-a, c) AM.NA.023-a, d) line drawing of AM.NA.023-a. Scale bars = 1 cm.

Intercostal tertiary veins are rarely preserved for this morphotype. The specimen with the greatest intercostal tertiary vein preservation is AM.NA.023-a (Figure 3.31-c). The intercostal tertiary veins are percurrent with courses that can be nearly straight or sinuous. The angle of the tertiary veins is obtuse, and exmedially they range from 105 ° to 144 ° (mean 119 °). The epimeidal tertiary veins are percurrent with a variable proximal course that can be perpendicular or parallel to the midvein. The distal course of the epimeidal tertiary is unclear due to limited preservation, but appears to parallel to intercostals tertiary veins.

The margin of AM8 is distinctive and is quite unlike any other leaf type from Allt Mor. The teeth are relatively large and extend away from the margin for some distance in the central part of the laminar, they become smaller towards the apex (Figures 3.30-a, c, e and 3.31-a). Typically the distal and proximal flanks are straight, which gives the tooth a distinctive triangular shape. The flanks of the teeth have different length, the distal flanks are approximately one third the length of the proximal flanks (Figure 3.31-a).

The teeth are primarily of a single order, they show little range in sizes, except for a slight decrease in scale towards the proximal and distal portion of the laminar. A single specimen (NMS.G.2002.64.5-a) has a smaller tooth emerging from the proximal flank of the superajcent a tooth (Figure 3.30-h). The presence of this smaller tooth indicates that AM8 had up to two orders, but the majority of the teeth appear to be first order. The teeth are supplied by a principal vein that curves inside the tooth and terminates at its apex.

3.15.6 Similarities to other fossil taxa

Fossil leaves associated with *Platycarya* have not been reported from the Paleocene, the earliest records of this genus are fruits from the Early Eocene of Europe and North America (Reid and Chandler 1933, Wing and Hickey 1984, Manchester 1987). The morphology of AM8 is remarkably similar to modern *Platycarya*, which suggests that its related to this modern genus. The leaves of AM8 along with associated pollen in the BTVP may therefore represent one of the earliest records of *Platycarya*.

Two Eocene species ascribed to *Platycarya*, *P. americana* and *P. castaneopsis* occur in association with *Platycarya* fruits from Wyoming and Dakota (Wing and Hickey 1984). The leaves of these two forms are markedly different to AM8 particularly in their base shapes and margin strcutre. The leaves of *P. americana* have an acute base angle with a straight base shape and its margin is finely serrate. The leaves of *P. castaneopsis* also have an acute base angle and straight base shape, the margin of this species has more prominent teeth, but they appear to be more irregular in shape and spacing, and nearly denate. These differences in base and margin form indicate that these leaf types are quite unlike AM8. Manchester (1987) suggested that although the fruits found at these localities represent ancestral members of the *Platycarya*, the associated leaves were unlike those of this genus and may represent distinct genera, a view also shared by Boulter and Kvacek (1989).

Platycarya pollen (*Platycaryapollenites*) is used as a zone taxa for the Late Paleocene to Early Eocene in the Northern Hemisphere, particularly in North America where it becomes abundant and widespread during this interval (Wing 1984). The presence of this pollen type in the mid Paleocene of the BTVP (Jolley 1997), suggests it may have originated in this region, or elsewhere in Europe. The relatively sudden appearance of this pollen type in the Late Paleocene of the Northern Hemisphere may indicate that it had migrated from Europe through the North Atlantic Igneous Province (NAIP) and into the Arctic, where it spread throughout the Northern Hemisphere.

3.15.7 Similarities to modern taxa

As previously stated in section 3.15.3, AM8 appears remarkably similar to the modern genus *Platycarya* of the Juglandaceae. It shares the same overall form, venation patterns and leaflet attachment. The absence of *Platycarya* reproductive structures from the BTVP prevents an accurate assignment to this modern genus, and so AM8 is regarded as "*Platycarya* cf" until these structures can be found. One of the oldest unequivocal records of this genus are fruits of *Platycarya richardsoni* from the Early Eocene London Clay of southern England (Reid and Chandler 1933). These fruits indicate that members of this genus had appeared by the Early Eocene and AM8 may represent an ancestor or related species to those from the Eocene in southern England.

3.16 Angiosperm morphotype 9 (AM9)

3.16.1 Specimen numbers

The specimen numbers of this morphotype are AM.NA: 059-a, 224, AM.NA.2008: 009-a, 013-a, NMS.G.2004.29: 30-a, 039, 098-b, NMSG.2002.64.3-j.

3.16.2 Diagnosis

Leaf attachment petiolate, blade attachment marginal. Laminar size notophyll-mesophyll, laminar length:width ratios ~1:1, laminar shape ovate, medial symmetry unclear possibly asymmetric, base symmetry unknown, unlobed margin crenate-serrate. Apex angle obtuse, apex shape convex or acuminate shape without a drip tip, base angle reflex, base shape cordate. Primary venation basal actinodromous, naked basal veins absent, five to seven basal veins present, agrophic veins compound. Major secondary veins semicraspedodromous, interior secondary veins absent, minor secondary veins semicraspedodromous, major secondary spacing irregular, secondary angle inconsistent, major secondary attachment excurrent. Intersecondary veins absent. Intercostal tertiary vein fabric alternate percurrent to mixed percurrent with obtuse vein angle. Epimedial tertiary veins alternate percurrent with proximal course acute to midvein and distal course parallel to intercostal tertiary. Higher order vein fabric not preserved. Tooth spacing regular, with two orders of teeth, 3 teeth per/cm, sinus shape rounded. Tooth shape convex/convex. Principal vein course unclear, tooth apex simple but indented.

3.16.3 Identification

Angiosperm morphotype 9 (AM9) is a relatively rare leaf type within the Allt Mort assemblage but includes one specimen that is nearly complete and others that have either well preserved venation margins or bases. This morphotype is characterised by its ovate to elliptic shape, strongly cordate base, basal actinodromous primary, semicraspedodromous secondary venation and crenate serrate margin. This morphotype shares a strikingly similar to *Vitiphyllum sewardii* of Ardtun, Mull (Boulter and Kvacek 1989).

Vitiphyllum sewardii laminar shapes are ovate, which corresponds to the morphology of AM9. Laminar length:width ratios are comparable and are ~1:1 or <1:1. The apexes of both leaf types have obtuse apex angles with shapes that are either convex or acuminate without a drip tip. Base shape is uniformly cordate with a reflex angle. The cordate bases have a long and broad basal sinus, which is characteristic of AM9 and *Vitiphyllum sewardii.* The bases of *Vitiphyllum sewardii* have an asymmetric basal extension, where one of the basal lobes is larger than the other. This feature has not been observed in the Allt Mor specimens due to the partial preservation of the base.

The primary, secondary and tertiary venation of both leaf types is consistent as both have basal actinodromous semicraspedodromous arrangement with alternate percurrent-opposite percurrent tertiary veins. Both leaf types also have compound agrophic veins and five to seven basal veins present.

The margin of AM9 is one of its defining characteristics, with its simple crenate-serrate teeth that have convex distal and proximal flanks. Two teeth orders are present; the first order is the least frequent and is supplied by lateral primary veins. The first order teeth are two to three times larger than the secondary teeth and often extend for some distance, giving the leaf a near lobate form. The second order teeth are approximately the same shape as the first order teeth and are widely spaced. This same marginal configuration is identical to *Vitiphyllum sewardii* of Mull.

The strong morphological similarities in overall leaf form, venation and margin between these two leaf types indicates they represent the same species. AM9 is therefore identifed as *Vitiphyllum sewardii.*

3.16.4 Discussion

The leaves of AM9 vary in their degree of fragmentation. Most of the leaf specimens are small fragments but one specimen (e.g. AM.NA.059-a) is nearly complete (Figure 3.32-a). This morphotype appears to be characterised by large leaves, even the highly fragmented specimens have fragmented areas of 2500 mm^2 to $3500mm^2$. The most complete specimen, AM.NA.059-a has an estimated original laminar area of 4200 mm^2. These laminar area measurements suggest that the leaves were notophyll to possibly mesophyll in size. These size estimates are lower than Ardtun specimens of this leaf type, which are within the mesophyll to megaphyll size range.

Laminar L:W ratios are difficult to determine for most specimens due to fragmentation, but AM.NA.059-a is complete enough to estimate at ~1:1. Laminar shape is unclear due to fragmentation, but the curvature of the laminar indicates the leaves were originally either ovate or elliptic (Figures 3.32-a, c and 3.33-c).

Apex morphology of this morphotype is known from two specimens (AM.NA.059-a and NMSG.2002.64.3-j) have different apex shapes. The shape of AM.NA.059-a is convex while NMSG.2002.64.3-j has a more accuminate apex that lacks a drip tip (Figures 3.32-a and 3.33-c). The apex angle is obtuse for both specimens, irrespective of apex shape. Basal preservation is limited two specimens (AM.NA.2008.012-a, NMS.G.2002.64.3-j), have cordate base shapes with a reflex angle of ~250° (Figure 3.33-a, c).

The secondary venation of this morphotype is distinctive. The major semicraspedodromous veins are branched or forked, and form loops with adjacent secondary or primary veins near to the margin. Secondary vein spacing appears to be fairly inconsistent along the outer primary veins but increases proximally in the central primary vein. Secondary vein angles are difficult to determine for most specimens due to fragmentation or limited preservation, but one specimen (AM.NA.2008.012-a) has sufficient preservation to determine the vein angles. The major secondary veins diverge from the central primary with angles of 39° of 49° and appear relatively uniform, the secondary veins on the outer primaries are not preserved in AM.NA.2008.012-a so it is impossible to gauge if they have inconsistent angles like other specimens of this morphotype.

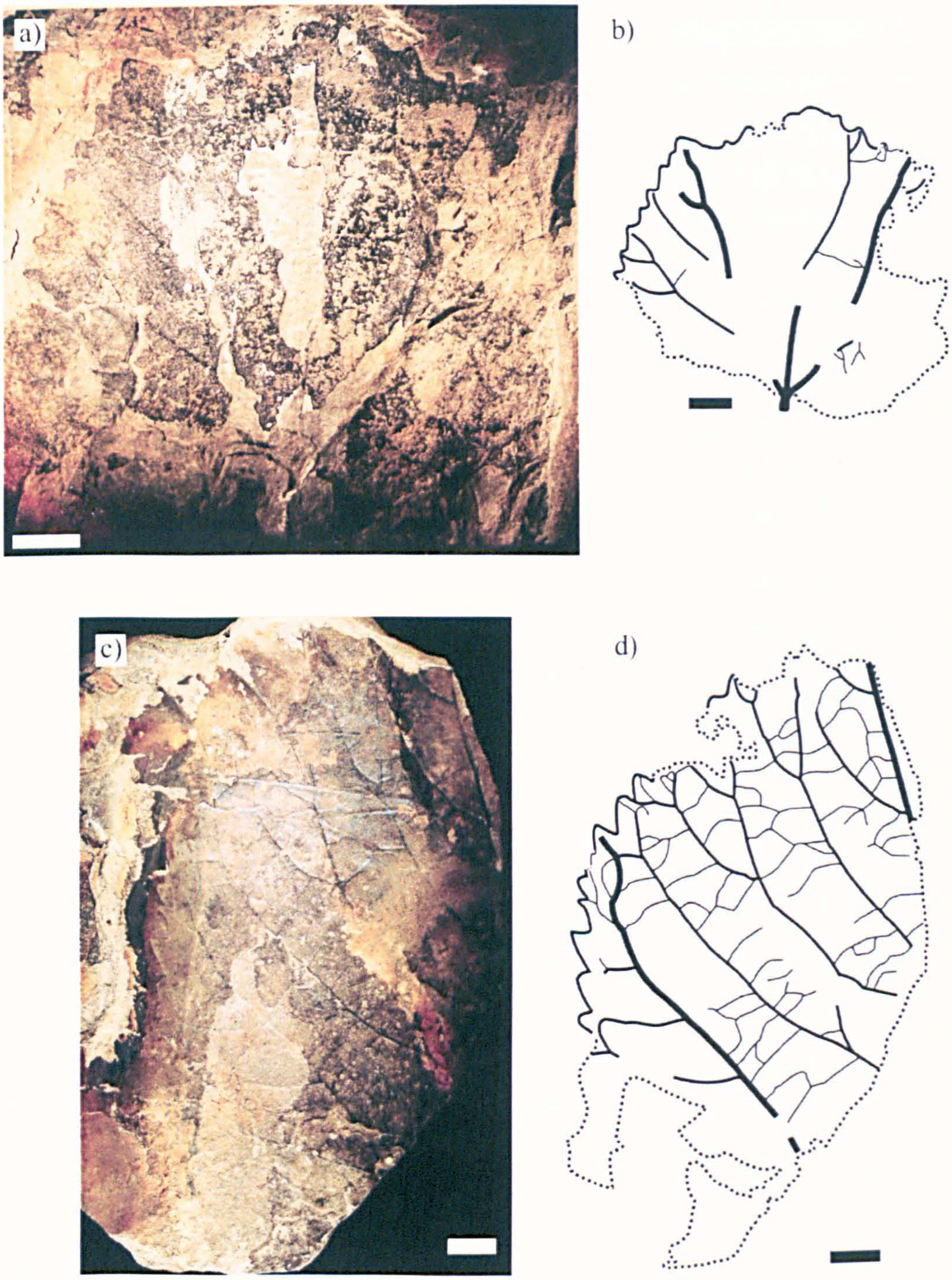

Figure 3.32. Specimens of AM9. a) AM.NA.059-a, b) line drawing of AM.NA.059-a, c) AM.NA.224, d) line drawing of AM.NA.224. Scale bars = 1 cm.

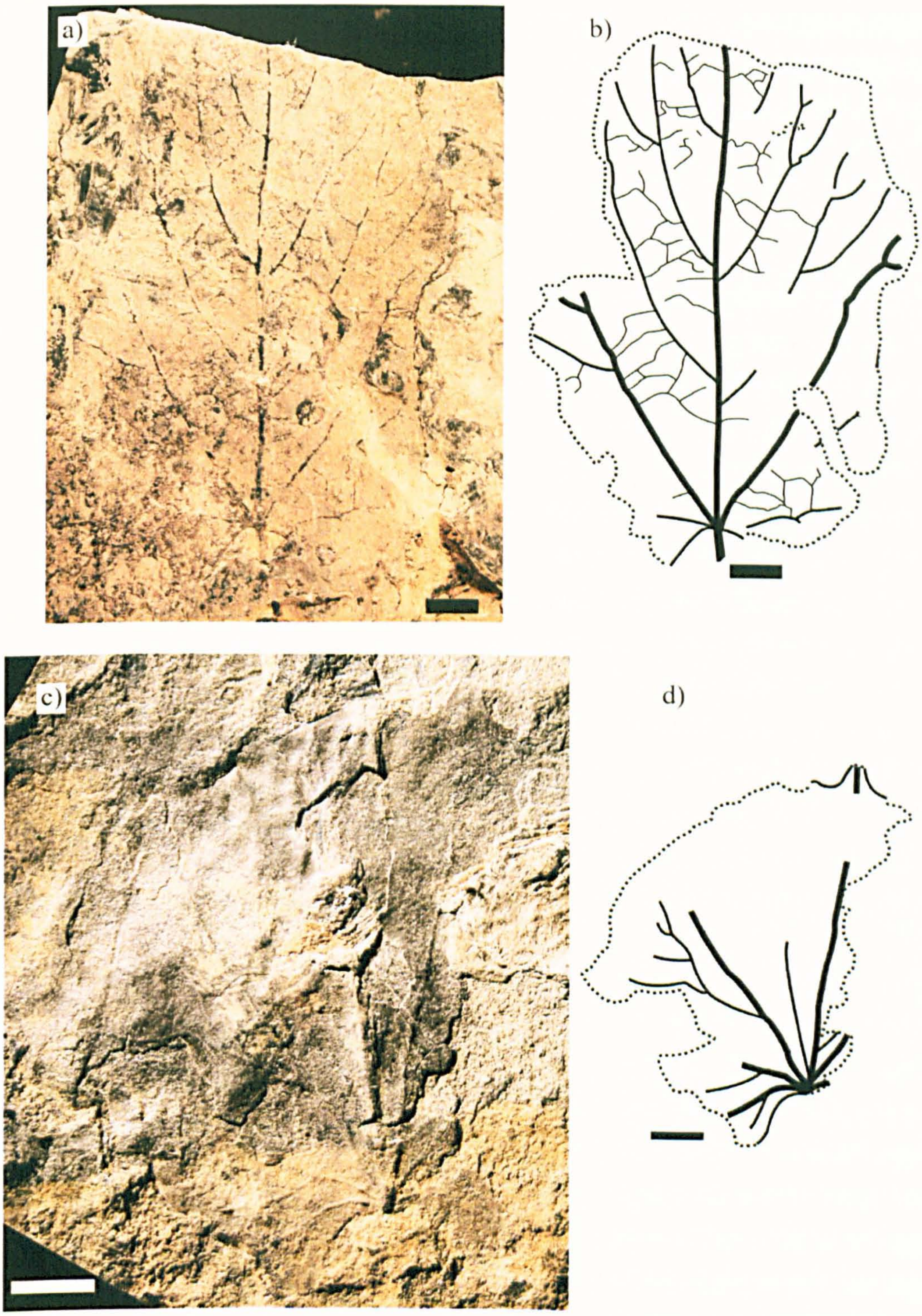

Figure 3.33. Specimens of AM9. a) AM.NA.2008.012-a, b) line drawing of AM.NA.2008.012-a, c) NMS.G.2002.64.3-j, d) line drawing of NMS.G.2002.64.3-j. Scale bar = 1 cm.

The intercostal tertiary veins are primarily alternate percurrent, but some are opposite percurrent and have sinuous courses. Intercostal vein angle variability is difficult to access for this morphotype as the specimen with most complete and clear tertiary venation, AM.NA.224, lacks the majority of its laminar area. The epimedial tertiary veins are alternate percurrent and have proximal courses that are acute to the midvein and have distal courses that are parallel to midvein. Due to the limited number of specimens with tertiary preservation it is difficult to determine if there is variability in epimedial tertiary venation.

The margin of AM9 is distinctive and a key characteristic of this morphotype. Only two specimens have teeth preserved, (AM.NA.59-a and AM.NA.224), AM.NA.59-a has the most intact margin and most complete teeth (Figure 3.32-a, c). The margin of AM.NA.224 although reasonably complete appears to be fragmented and the teeth partially preserved making them difficult to access. The proximal and distal flanks of the teeth are convex but their lengths vary, typically the proximal flanks of the teeth are two to three times longer than that of the distal flanks. The teeth of AM9 are primarily simple, but the teeth with principal veins supplied by the outer primary veins are larger and appear to be compound with two orders of teeth. These larger teeth give the leaf an almost palmately lobed appearance, but the sinus between the veins is weakly developed so this morphotype is not considered to be lobed. A notable feature of some of the teeth of AM.NA.59-a are their indented apices (Figure 3.32-a). The structure of these indentations is not clear. There does not appear to any cavities or opaque tissues associated with them. Principal veins supply both tooth orders and appear to be derived from the primary, secondary and tertiary veins.

3.16.5 Similarities to other fossil taxa

Leaves associated with *Vitiphyllum* are relatively rare in the Paleocene and have only been described from Mull, Svalbard and Greenland (Boulter and Kvacek, Kvacek et al. 1994, Birkenmajer and Zastawniak 2005). The latter was originally assigned to *Acer* but is regarded currently as *Vitiphyllum* (Kvacek et al. 1994, Birkenmajer and Zastawniak 2005). A more recent collection from Svalbard by Birkenmajer and Zastawniak (2005) has provided more *Vitiphyllum*-like foliage. The specimens collected are poorly preserved and highly fragmented, preventing an accurate comparison. These specimens do not have any margin or apexes preserved and have poor venation clarity, but it is clear that they are not similar to BTVP forms. These leaves either represent another species of *Vitiphyllum* or another genus entirely. Additional better preserved specimens are required to improve its systematic position and determine whether they are comparable to the BTVP forms.

Other Vitaceae-like foliage is reported from the Paleocene of west Greenland. The Greenland specimens described by Koch (1966) of *Vitis olriki* share some characters in common with *Vitiphyllum*, particularly the venation and the base shape. These leaves are distinct from

Vitiphyllum sewardii, however, in that they are more elongate with a more acute apex and have far fewer teeth. These two leaf types may be related but appear to represent distinct species associated with the Vitaceae.

Boulter and Kvacek (1989) discussed the similarities of *Vitiphyllum* with fossil representatives of the Vitaceae, and found that *Vitiphyllum sewardii* was unlike other Paleogene members of this group. This suggests that this leaf type may represent an endemic form of the Vitaceae that may be related to species in Greenland and Svalbard.

3.16.6 Similarities to modern taxa

Boulter and Kvacek (1989) discussed the affinities of *Vitiphyllum sewardii* in relation to modern families and concluded that this leaf type may represent a member of the Vitaceae based on its form, margin and venation characteristics. They did, however, refrain from formally associating it with the modern genus *Vitis* based on the absence of seeds or other reproductive structures (Boulter and Kvacek 1989). The Mull and Skye specimens of *Vitiphyllum* are probably representatives of the Vitaceae but without preserved reproductive structures the association to this family is tentative. If AM9 (*Vitiphyllum sewardii*) is a member of the Vitaceae it may represent a woody vine, which is a common habit of this family (Gianoli 2004). The other angiosperm morphotypes of the BTVP appear to represent woody shrubs or trees (Boulter and Kvacek 1989, Jolley 1997, Jolley et al. 2009). *Vitiphyllum sewardii* therefore seems to represent the only plant with a liana habit in the BTVP.

3.17 Angiosperm morphotype 10 (AM 10)

3.17.1 Specimen numbers

The specimen numbers of this morphotype are: AM.NA.2009: 026-a, NMS.G.2005.145.013-b.

3.17.2 Diagnosis

Laminar size microphyll to notophyll, laminar L:W ~2:1, laminar shape elliptic, medially symmetrical, base appears symmetrical, unlobed, margin entire. Apex angle acute, apex shape acuminate forming a drip tip, shape unclear appears convex, base shape unclear possibly convex. Primary venation pinnate, presence of naked basal veins and number of basal veins unknown, agrophic veins absent, minor secondary veins absent. Major secondary veins eucamptodromous, interior secondary veins absent, minor secondary veins absent, major secondary spacing decreasing proximally, secondary angles range uniform. Intercostal tertiary vein fabric opposite percurrent. Epimedial tertiary veins not preserved. Higher order venation not visible.

3.17.3 Identification

Angiosperm morphotype 10 (AM10) is a rare component of the Skye flora, but specimens of the this morphotype have been identified from Allt Mor and Glen Osdale, and possibly from Allt Geodh' a' Ghanhna, suggesting it was widespread in riparian environments on Skye. This morphotype shares many characteristics in its overall leaf form, venation and margin characteristics with fossil leaves of *Cornophyllum hebridicum* from Ardtun, Mull. Specimens of from both localities appear to have elliptic laminar shapes and have approximate L:W ratios of ~2:1 to 2.5:1. Despite the limited preservation of the margin in the Mull specimens it appears to be entire as do the specimens from Allt Mor and Glen Osdale, although several of the Allt Mor specimens (e.g. AM.09.L4.28-a and AM.09.L4.0036-a) appear to have slightly erose edges in the upper portion of the laminar. Apex shape is similar as both leaf types have well developed acuminate apexes that form a prominent drip-tip.

The venation of AM10 appears identical to *Cornophyllum hebridicum* of Ardtun, and both share the same characteristic pinnate eucampatodormous arrangement. The basal eucamptodromous secondary veins curve steadily towards the apex and follow the edge of the margin for some distance. The more distal secondaries are less numerous and more widely spaced. Another distinctive similarity between these two leaf types is the course of the distal most secondary veins, which diminish in gauge and extend up the apex adjacent to the leaf margin. The tertiary venation of AM10 is poorly preserved but appears to be similar to *Cornophyllum hebridicum* as both have opposite percurrent intercostal veins that are widely spaced.

The close similarity in the laminar form, venation and margin of AM10 with *Cornophyllum hebridicum* suggests that these two leaf types represent the same species, AM10 is therefore regarded as *Cornophyllum hebridicum.*

3.17.4 Discussion

This morphotype is represented by a limited number of specimens, but these have enough morphological characters preserved to differentiate it from other morphotypes and provide an understanding of the overall form of this morphotype. The most complete specimens of AM10, (AM.NA.2009.026-a and NMS.G.2005.145.013-b) (Figures 3.34-a and 3.35-a) have an estimated laminar areas of 1452 mm^2 and 1785mm^2 respectively, which indicates their original laminar size class was microphyll. The L:W ratio of the laminar is difficult to determine from the fragmented specimens, but is estimated to have been ~2:1 to 2.5:1. Laminar shape is unclear but based on the curvature of the margin and vein course it appears to be elliptic.

Medial symmetry is variable and appears to be related to the course of the primary vein. Leaves that have primary veins with a straight course are medially symmetric (e.g.

NMS.G.2005.145.013-b), while leaves with curved primary course are slightly asymmetric (e.g. AM.NA.2009.026-a).

The margin appears entire, specimen NMS.G.2005.145.013-b has the most complete margin which extends from the base to approximately the middle of the laminar, appears to be entire for its entire preserved length (Figure 3.34-a). Specimen AM.NA.2009.026-a has margin preserved along the distal portion the laminar and along the apex and appears to be entire except for a small projection (Figure 3.35-a). Careful examination of this projection indicated that it was not a tooth as it appeared to lack any supporting venation, and may be a artefact of preservation or an undulation in the entire margin.

The apex of AM.NA.2009.026-a acute, its shape appears to be acuminate forming a distinct drip tip structure. The base of this morphotype is not preserved but margin near the base suggests its angle have been acute and had a convex shape (Figure 3.35-a).

The major secondary veins of this morphotype are eucamptodromous, which is not seen in other morphotypes from Skye. The major secondary vein spacing in the lower, central, and basal portion of the laminar gradually decreases. Secondary vein angle variability across the laminar ranges from being appears to be uniform, vein angle measurements from NMS.G.2005.145.013-b are 47 ° to 52 ° in the central portion of the laminar and proximally range from 49 ° to 52 °. The intercostal tertiary veins are poorly preserved but appear to be opposite percurrent with a primarily straight course, and widely spaced.

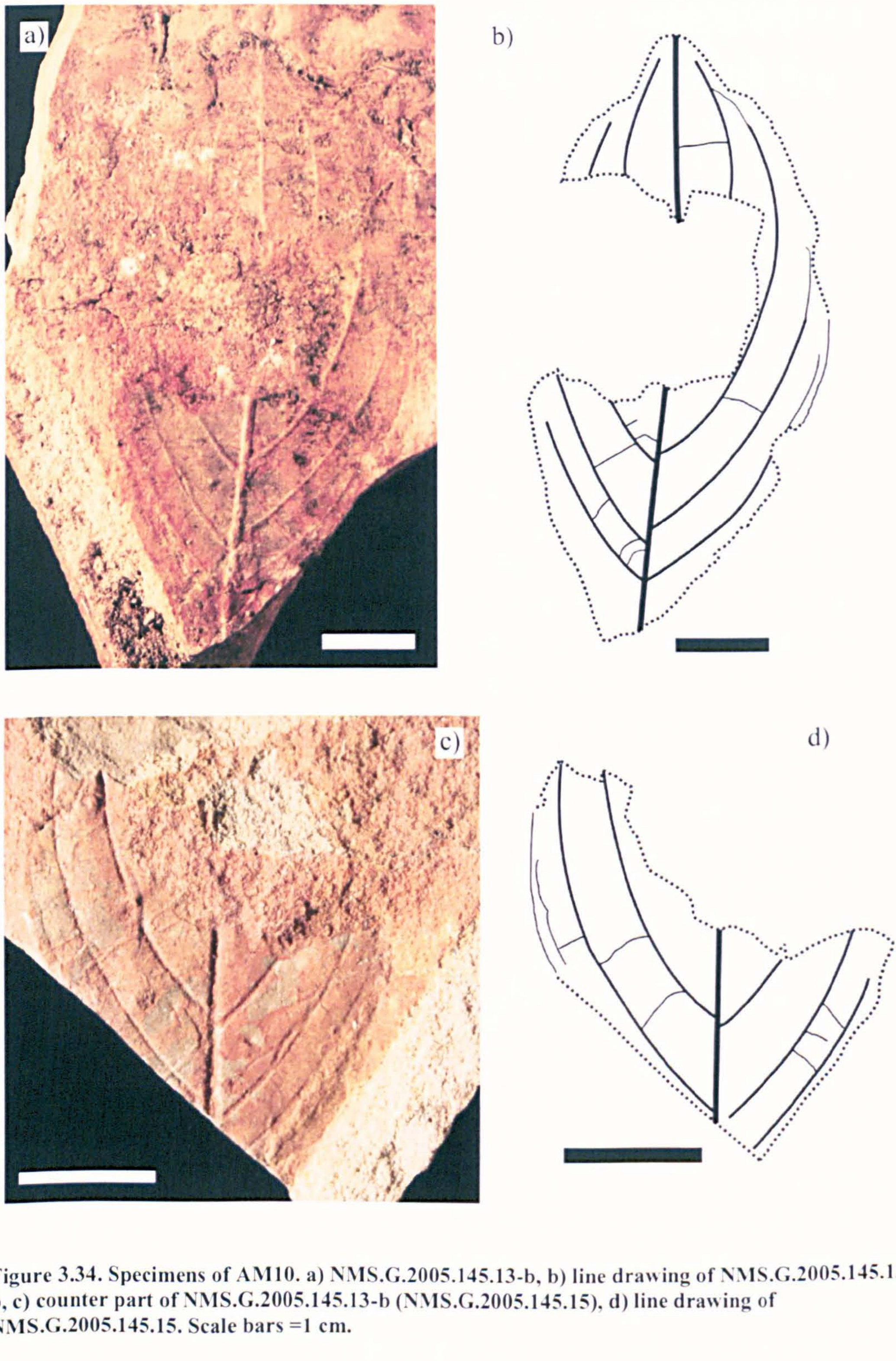

Figure 3.34. Specimens of AM10. a) NMS.G.2005.145.13-b, b) line drawing of NMS.G.2005.145.13-b, c) counter part of NMS.G.2005.145.13-b (NMS.G.2005.145.15), d) line drawing of NMS.G.2005.145.15. Scale bars =1 cm.

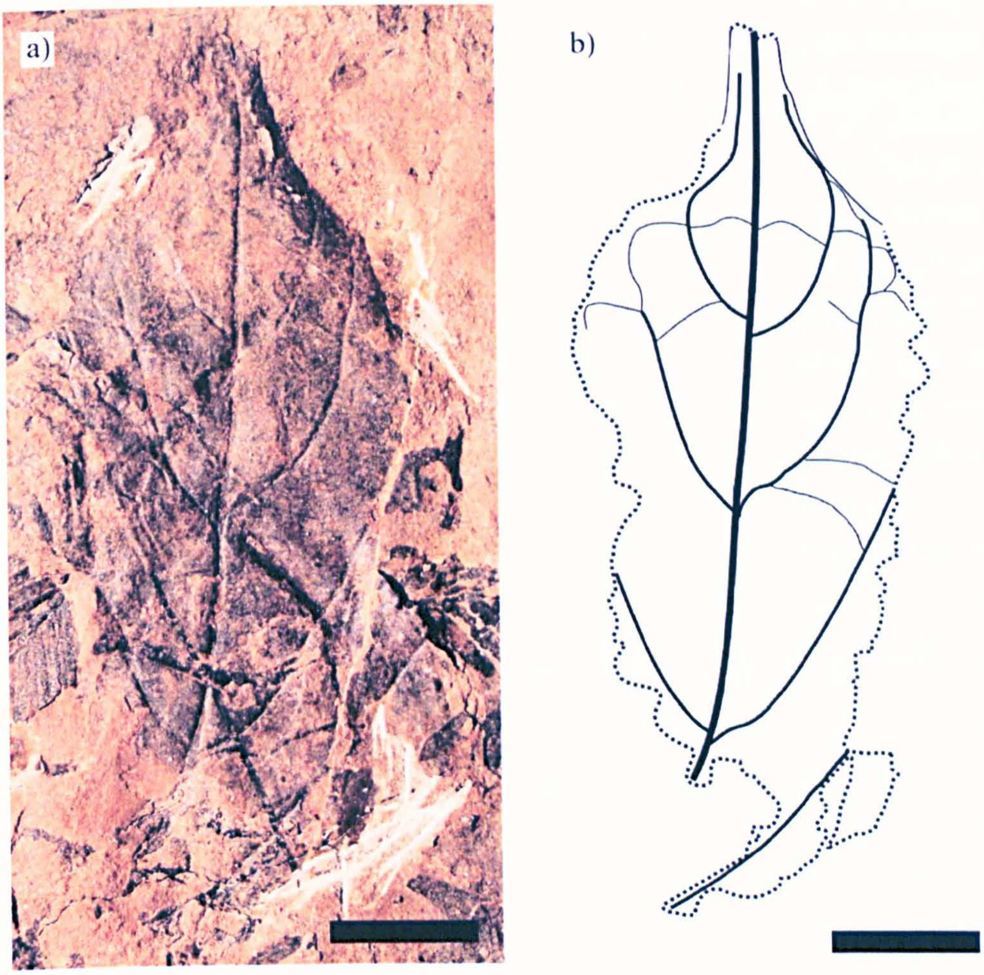

Figure 3.35. Specimen of AM10. a) AM.NA.2009.026-a, b) line drawing of AM.NA.2009.026-a.

3.17.5 Similarities to other fossil taxa

A comprehensive review of the affinities and morphology of *Cornophyllum* was carried out by Manchester et al. (2009) who studied leaf material from the United States of America, Russia, Scotland and Greenland. This study has confirmed that at least some species of *Cornophyllum* are attributable to the modern genus *Cornus*, which has distinctive trichome morphology. *Cornus swingii* is a newly described Paleocene reprehensive of the Cornaceae and has been found in several localities in Montana, Wyoming, North and South Dakota. This species is reliably placed in the modern genus *Cornus* because it has trichomes preserved that are characteristic of this modern genus (Manchester et al. 2009). Specimens of *Cornus swingii* figured by Manchester et al. 2009 indicate that it shares some similarities with *Cornophylllum hebridicum* (AM10) of the BTVP, but differs markedly in most respects. Both taxa share the same elliptic laminar shape, entire, slightly erose margin in the upper portion of the laminar and has eucamptodromous secondary veins. The major differences between *Cornus swingii* and *Cornophyllum hebridicum* includes its broader length:width ratio, the lack of a acuminate apex with drip-tip, and it has three to five pairs of secondary veins opposed to four or five in *Cornophylllum hebridicum.*

Cornus swingii distribution is broad across the western interior of the United States, but Manchester et al. (2009) noted its occurrence is patchy and is restricted to a few sites within this range, but where it does occur it is an abundant element of the flora. This distribution pattern seems to be similar for *Cornophyllum newberryi*, which is putatively associated to the Cornaceae (Bercovici et al. 2008). Specimens of *Cornophyllum newberryi* described by Bercovici et al. (2008) share many characteristics with *Cornophyllum hebridicum*, as their laminar shape is elliptic, the apex is acuminate, the margin is entire and the venation is broadly similar. There are key differences between these taxa, however, as *Cornophyllum newberryi* has a greater number of secondary veins which are spaced fairly evenly across the laminar, the course of secondairy veins is less curved, and the secondary vein angle appears more obtuse compared to *Cornophyllum hebridicum.*

The Paleocene Atanikerdluk locality of Greenland also contains leaves associated to *Cornus*, *Cornus hyperborea* (Manchester et al. 2009). The venation characteristics of *Cornus hyperborea* indicate that it has an affinity with the Cornaceae, but the characteristic *Cornus* trichomes are not preserved, and it therefore cannot be considered definitively as *Cornus* (Manchester et al. 2009). The highly fragmented specimens of *Cornus hyperborea* figured by Manchester et al. (2009) are too poorly preserved to establish whether this taxon was similar to *Cornophyllum hebridicum.* Manchester et al. (2009) noted that both *Cornus hyperborea* and *Cornophyllum hebridicum* have secondary veins that originate in the basal or central portion of the laminar and are infrequent more distally, which may suggest that they are similar.

The European record of *Cornus* includes the previously mentioned *Cornophyllum hebridicum* of the BTVP and *Cornus platyphylla* from the Late Paleocene of Sézanne, France. Specimens of *Cornus platyphylla* described in Manchester et al. (2009) show remarkable similarities to *Cornophyllum hebridicum* in its laminar form, margin and venation characteristics. It does, however, differ to *Cornophyllum hebridicum* in that it has at least five pairs of secondary veins. The close morphological relationship between these two taxa and their close geographical and age suggests that these taxa may share a possible common ancestor.

Two Asian species are described in Manchester et al. (2009), *Cornophyllum swindiiformis* and *Cornus krassilovii.* The single specimen of *Cornophyllum swindiiformis* figured by Manchester et al. (2009) shows its venation patterns in the basal-central portion of the laminar are broadly similar to *Cornophyllum hebridicum.* The basal morphology of *Cornophyllum swindiiformis* is much broader with a more obtuse base angle compared to *Cornophyllum hebridicum. Cornus krassilovii* has the characteristic *Cornus* trichomes and is therefore considered as member of this modern genus (Manchester et al. 2009). *Cornus krassilovii* differs significantly to *Cornophyllum hebridicum* in regards to its secondary veins which form loops at their extremities, a feature not observed in the BTVP forms.

It appears that members of the Cornaceae, including members of the modern genus *Cornus* were present and, indeed, widespread in the Paleocene. *Cornophyllum hebridicum* may be distantly related to these species, but appears to be most closely related to *Cornus platyphylla* from the Late Paleocene of Sézanne, France.

3.17.6 Similarities to modern taxa

Boulter and Kvacek (1989) accessed the similarities of *C. hebridicum* with modern taxa; the limited preservation and low number of the specimens they studied prevented them from making a firm association with modern taxa. Indeed they questioned whether the Cornaceae was present in the Cretaceous or early Paleogene (Boulter and Kvacek 1989).

Manchester et al. (2009) has shown that that not only was the family Cornaceae present but that the modern genus *Cornus* was already established in the Paleocene. The presence of the characteristic calcified trichomes, unique to Cornaceae are present in at least two species, *Cornus swingii* of the US and *Cornus krassilovii* of Russia. Manchester et al. (2009) did not re-examine the Ardtun specimens of *Cornophyllum hebridicum* and were therefore unable to determine if this species was a member of the genus *Cornus*.

Further investigation of whether trichomes were present for both the Skye and Mull specimens of *Cornophyllum hebridicum* is required to access if they are representatives of *Cornus*. Therefore it is prudent to retain the form genus *Cornophyllum* for the BTVP forms until it can be shown that they have calcified trichomes, *Cornophyllum hebridicum* (AM10) is therefore tentatively associated to the family Cornaceae but has an undetermined generic affinity.

3.18 Angiosperm morphotype 11 (AM11)

3.18.1 Specimen numbers

The specimen numbers of this morphotype are: AM.NA: 173, 219-b, AM.NA.2008.012-b, NMS.G.2004.29: 0.23-a, 024-d, 035-a.

3.18.2 Diagnosis

Leaf attachment petiolate. Blade attachment marginal, laminar size microphyll, laminar L:W ratio ~1:1, laminar shape appears ovate, elliptic or obovate, blade medially symmetrical, base symmetry unknown, unlobed, margin crenate-serrate. Apex angle unknown, apex shape unclear appears convex or acuminate without a drip-tip, base angle reflex or possibly obtuse, base shape cordate or possibly truncate. Primary venation basal actinodromous, naked basal veins absent, six to eight basal veins, agrophic absent. Major secondary veins appear semicraspedodromous, interior secondary veins absent, minor secondary vein course unclear possibly semicraspedodromous, major secondary spacing abruptly increasing proximally, secondary angle inconsistent, major secondary attachment excurrent or decurrent. Intersecondary veins absent. Tertiary, and higher order venation not visible. Tooth spacing irregular, two orders of teeth, 3 teeth per/cm. Sinus shape rounded, tooth shape convex/convex.

3.18.3 Identification

In overall appearance angiosperm morphotype 11 (AM11) resembles AM2 (*Trochodendroides*) in its overall leaf form and its venation pattern, which may indicate that AM11 represents a second species of *Trochodendroides*. It does, however, differ to AM2 as its base shape, degree of bifurcation and number of loops of the secondary veins, and its margin is markedly different. Fossil leaves of *Zizyphoides* appear to be the closest match morphologically to AM11, two species *Z. auriculata* and *Z. flabella* share many morphological similarities with AM11 (Crane et al. 1991, Manchester et al. 1991). Both of these species are highly polymorphic in their leaf form, margin and venation patterns, which appears to be the case for AM11.

The Miocene form, *Z. auriculata* has a variable shape that can be ovate, elliptic or obovate, the base shape can be rounded, truncate, concavo-convex or nearly cordate with an obtuse to reflex base angle, the apex is convex or emarginated with an obtuse or acute angle. The margin has prominent crenulations (teeth) that are highly irregular, and in some specimens can appear nearly palmately lobed. The primary venation is basal actinodromous, and the primary veins are relatively narrow gauge, the major secondary veins are semicraspedodromous that form loops near to the margin. The morphology of AM11 is broadly similar to *Z. auriculata* as it appears to have similar laminar, base and apex shapes, its margin is also undulating and crenulated like *Z. auriculata* (Manchester et al. 1991). The primary veins of AM11 are similar to *Z. auriculata* but the secondary veins do not appear to form loops as frequently as *Z. auriculata*, and the secondary veins bifurcate readily in AM11.

Zizyphoides flabella, was a widely distributed species that appears in Paleogene leaf assemblages in North America, Greenland, Svalbard and Asia (Crane et al. 1991). The secondary venation characteristics of *Z. flabella* appear most similar to AM11, as its secondary veins bifurcate readily towards the margin. Like *Z. auriculata*, *Z. flabella* is highly polymorphic, some of these morphs have basal shapes similar to AM11, while others are rounded or have more acute basal angles. The margin of *Z. flabella* is often entire, no entire margined species of AM11 have been identified at Allt Mor. Morphs of *Z. flabella* with teeth have more rounded tooth shapes and have narrower tooth sinuses compared to AM11.

The morphological similarities of *Z. auriculata* and *Z. flabella* with AM11 indicates that this morphotype appears to be a representative of the genus *Zizyphoides*. The differences in morphology between these two described species and AM11 may be related to their polymorphism and the limited preservation of AM11, but may indicate that AM11 represents a distinct species. The limited preservation of this morphotype prevents a more detailed diagnosis of its higher order venation patterns, which could help to determine its identity. It is therefore tentatively considered to be an indeterminate species of this genus, *Zizyphoides* sp.

3.18.4 Discussion

As discussed in the previous section (3.18.3) the leaves of AM11 are polymorphic and display a wide variety of basal and margin differences, they can be recognised as the same morphotype, however, as their venation characteristics are similar. Specimens of AM11 whose original laminar area can be estimated are microphyll, and range from 1273mm^2 to 1712mm^2. Laminar length: width ratios are difficult to determine due to fragmentation of the specimens, but the most complete specimens (e.g. NMS.G.2004.29.024-d and AM.NA.173) appear to have L:W ratios of ~1:1. Lamina shape appears to be highly variable, but difficult to determine conclusively due to fragmentation. One specimen (AM.NA.173) appears elliptic, another ovate (NMS.G.2004.29.035-a) and one appears obovate (NMS.G.2004.29.024-d). Medial symmetry is unclear but it appears all specimens are symmetric (Figures 3.36-a, c, e).

Three specimens have partially preserved apexes, which indicate that this morphotype had two apex shapes. Two specimens of AM11 (NMS.G.2004.29.024-d and AM.NA.173) appear to have acuminate apexes that lack a drip-tip, another specimen (NMS.G.2004.29.035-a) appears to have a more convex apex shape. Base shape appears to be cordate for all specimens with bases preserved but the sinus is very broad which gives the base a near truncate or concavo-convex appearance (e.g AM.NA.173, AM.NA.2008.011-b and NMS.G.2004.29.024-d) (Figure 3.36-a, c, 3.37-a).

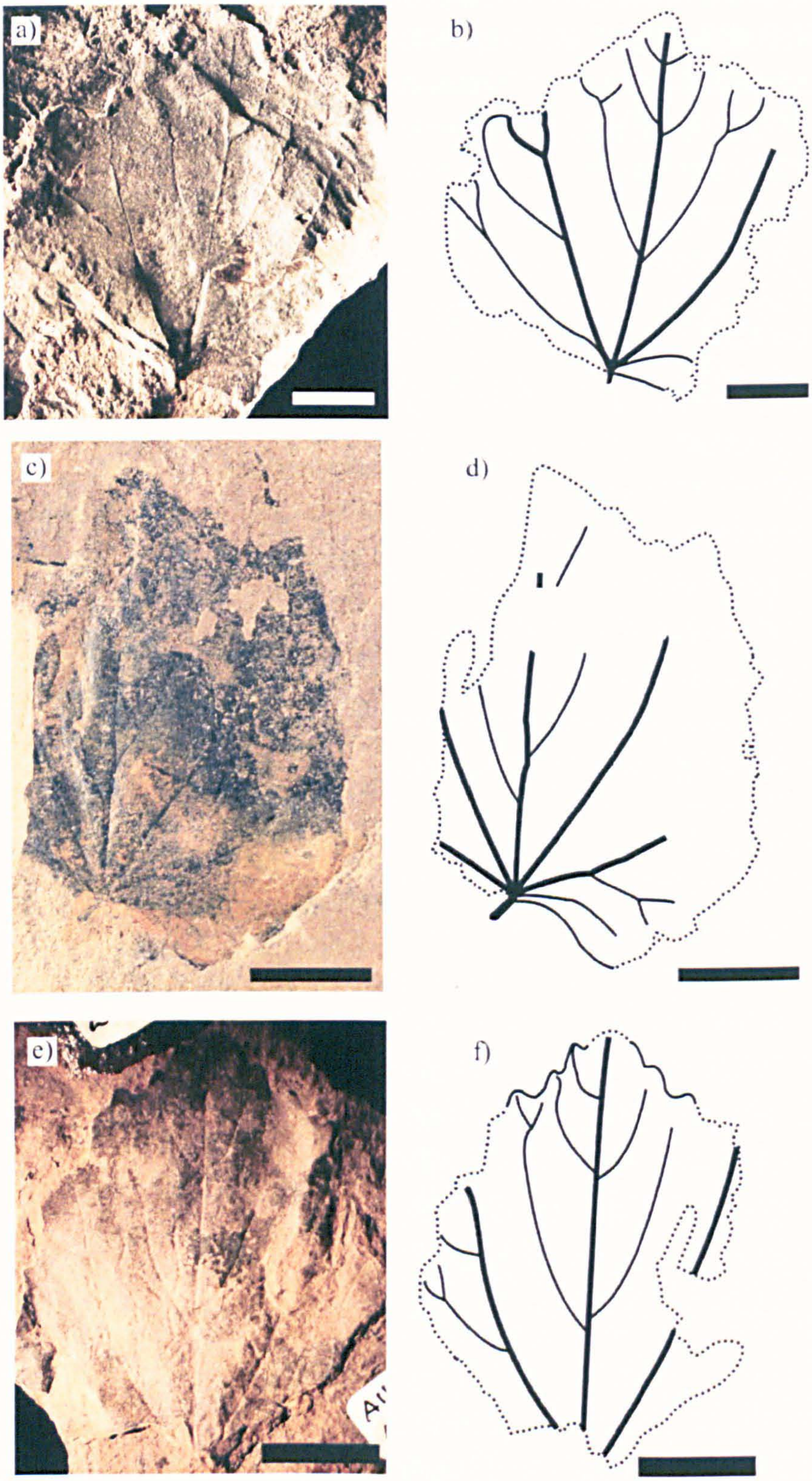

Figure 3.36. Specimens of AM11. a) NMS.G.2004.29.029-d, b) line drawing of NMS.G.2004.29.029-d, c) AM.NA.173, d) line drawing of AM.NA.173, e) NMS.G.2004.29.35-a, f) line drawing of NMS.G.2004.29.35-a. Scale bars =1 cm.

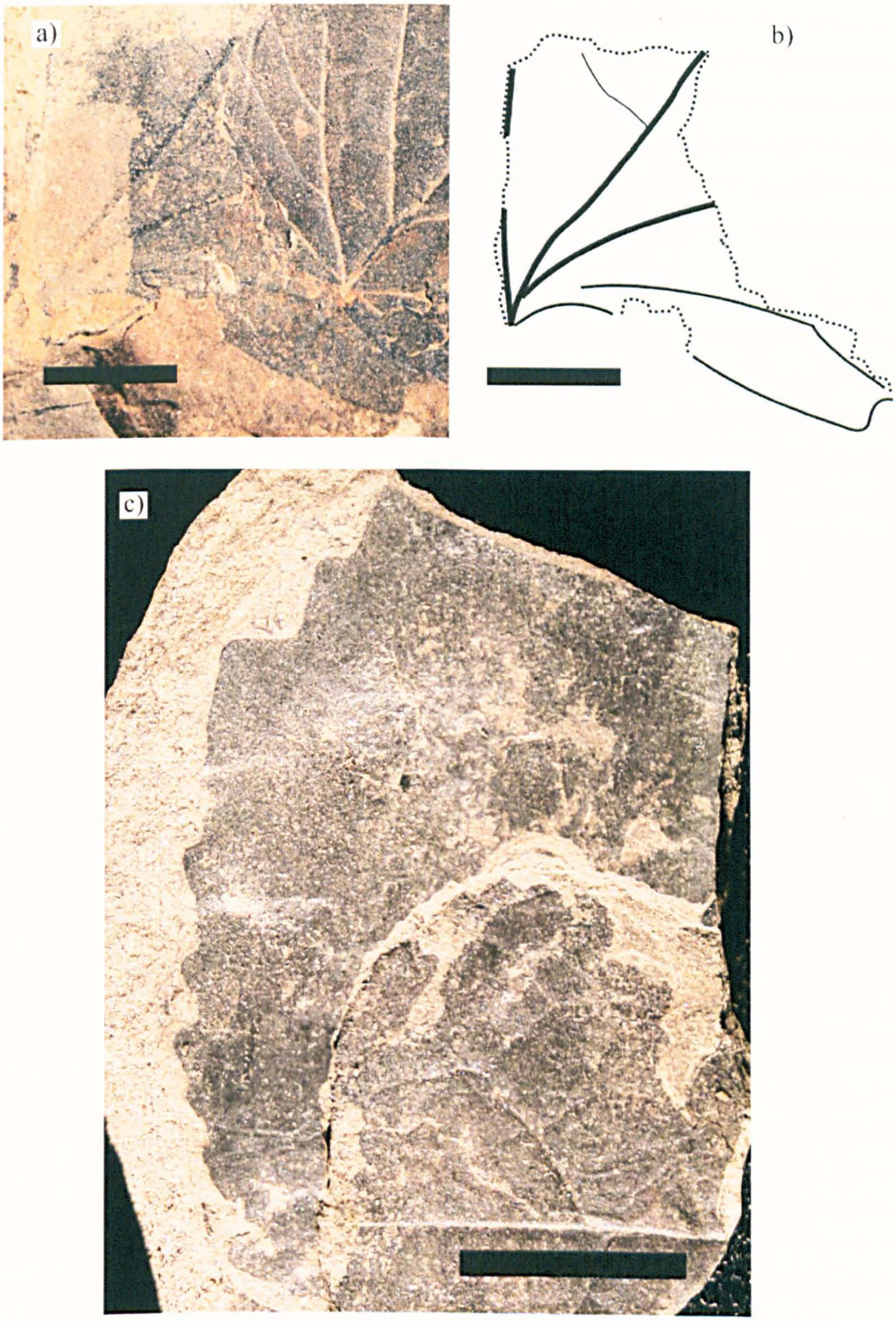

Figure 3.37. Specimens of AM11. a) AM.NA.2008.012-b, b) line drawing of AM.NA.2008.012-b, c) AM.NA. 219-b. Scale bars = 1cm.

The venation patterns of AM11 are difficult to determine as they are faintly preserved a trait that is shared with similar leaves from the Paleogene of Svalbard (Clifton 2010. pers.comm). The primary veins are reasonably well preserved and their course is well understood, the secondary veins are poorly preserved but show they form loops near the margin and bifurcate freely. The tertiary and higher venation is not preserved, which prevents an understanding of the higher order venation pattern of AM11. The five primary basal actinodromous have a variable course that can be nearly straight, curved or sinuous. These primary veins often fork near the margin, where they appear to become the principle veins for the teeth in the distal portion of the margin (Figure 3.36-a).

The margin of AM11 is distinctive, it is crenate-serrate and the teeth are well rounded with broad rounded sinuses (AM.NA.2008.011-b) (Figure 3.36-e). Specimen AM.NA.219-b (Figure 3.37-c) has a well preserved margin displaying several well preserved teeth and their sinuses, but has very poor venation clarity. The lack of venation clarity reduces the ability to identify, which morphotype it belongs to, the margin characterisitcs are similar to both *Zizyphoides* and *Vitiphyllum sewardii* (AM9). This specimen is regarded as a portion of *Zizyphoides* margin as the teeth lack the indentation at their apex, which is common in teeth of AM9, the tooth apex also appears blunter than the apexes of AM9. The teeth on specimen AM.NA.219-b show there are two tooth present, which is also common in leaves of *Zizyphoides auriculata,* and to a lesser extent *Zizyphoides flabella*. Tooth spacing is irregular and there are 2 to 3 teeth/cm. Tooth venation is difficult to determine due to limited preservation, but there does appear to be a principle vein that terminates at the tooth apex (AM.NA.2008.011-b).

3.18.5 Similarities to other fossil taxa

Determining the distribution of *Zizyphoides* from its leaves is hampered by its close resemblance to other leaf types, particularly *Cercidiphyllum*-like leaves such as *Trochodendroides*. This coupled with its high morphological variability may have given rise to numerous synonyms for the same taxon (Crane et al. 1991). Paleogene fossil leaves that have confidently been attributed to *Zizyphoides flabella* are in sequences from Svalbard, Asia and North America, which suggests that it was a common component of high to mid latitude floras in the Northern Hemisphere (Crane et al. 1991, Kvacek et al. 1994, Herman et al. 2009, Wang et al. 2009)

Leaves similar to AM11 (e.g. *Zizyphoides flabella*) are absent from the Ardtun floral assemblage of Mull, but, another species ascribed to this genus, *Zizyphoides ardtunesis* is present. This species, however, is very unlike other examples of this genus, its shape is more elongated and narrower, the apex is acute, the base is rounded and the margin is finely serrated (Boulter and Kvacek 1989). This species or one similar to it appears to be present in the Eocene of Svalbard and has been identified from new collections from the Aspelintoppen Formation (Clifton 2010 Pers. Comm). The morphology of *Zizyphoides ardtunensis* and its dissimilarity to other *Zizyphoides* leaf types indicates that it may represent another genus entirely.

Fossil leaves of *Zizyphoides flabella* from Svalbard indicate that it was present throughout much of the Paleogene, and occurs in the Early Paleocene Firkanten Formation and Ny-Alesund subgroup, the Early to Middle Eocene Aspelintoppen Formation, and the Middle to Late Eocene Renardodden Formation (Kvacek et al. 1994). As mentioned in section (3.18.3) AM11 appears similar to this species, and to specimens from Svalbard, which may indicate they may be related. Associated infructescences of *Zizyphoides*, *Nordenskioeldia borealis,* are present in the Paleocene of Svalbard (Kvacek et al. 2001).

Leaves of *Zizyphoides flabella* are an abundant element of the late Maastrichian and Danian Tsagayan Formation of the Amur Basin, and occur in both the Boguchan and Bureya floras (Herman et al. 2009). Danian to early Selandian floras of the Tsagayan Formation of Russia (Pioneer flora) and the Wuyun Formation (Wuyun flora), Heilongjiang Province, China have yielded a high abundance of *Zizyphoides flabella* leaves. Indeed, along with *Trochodendroides arctica* and *Tilliaephyllum tsagajanicum* these taxa collectively account for 50 to 75% of the leaf macrofossils recovered from the Pioneer and Wuyun floras (Herman et al. 2009). Elsewhere in Asia *Zizyphoides flabella* has been described from Kazakhstan, Japan and Mongolia, which suggests it was widely distributed in Asia (Crane et al. 1991).

North American Paleocene leaf records of *Zizyphoides flabella* indicate that it was also widespread in this continent and has been described from localities in Alberta, Alaska, Montana, Wyoming, North Dakota, Wyoming and Washington (Crane et al. 1991).

The associated fruits of *Zizyphoides*, *Nordenskioeldia*, have an excellent fossil record and are common in North America, Asia and Europe from the Late Cretaceous to Miocene (Crane et al. 1991, Manchester et al. 1991, Wang et al. 2009). Wang et al. (2009) compiled a comprehensive phytogeographic history of this plant based on the occurrence of the *Nordenskioeldia* infructescences from the Northern Hemisphere from the Late Cretaceous to the Miocene. The study by Wang et al. (2009) suggested that this plant evolved in Asia during the Cretaceous, and subsequently spread into North America and Europe during the Late Cretaceous and Paleocene.

Paleocene fossils of *Nordenskioeldia* indicate that its range expanded significantly during this interval with occurrences in Asia, North America, Greenland and Svalbard with a palaeolatitudinal range of 40 °N to 69°N (Wang et al. 2009). The Paleocene Asian record is extensive and includes localities in Russia, Mongolia, Japan, Kazakhstan and China (Wang et al. 2009). The American record is broad and covers several localities in the Western Interior of the US, Alaska, Alberta and the Northwest Territories (Wang et al. 2009). In the Arctic region *Nordenskioeldia* occurs in Greenland and Svalbard (Wang et al. 2009). The Paleocene migratory pathway into Eurasia was suggested by Wang et al. (2009) to have occurred across the North Atlantic prior to rifting of this land bridge. The presence of *Zizyphoides*-like leaves on Skye (AM11) during the mid Paleocene supports this Eurasian migratory route.

3.18.6 Similarities to modern taxa

Specimens of AM11 (*Zizyphoides sp.*) from Allt Mor provide little evidence for the association with a group due to their limited preservation. Leaves of *Zizyphoides flabella*, which is a possible relative of AM11 have described from North America in assocaiton with reproductive structures. Crane et al. (1991) noted that leaves of *Zizyphoides flabella* have similar venation patterns, long and short shoot morphology and the position of the gynoecium are typical of modern members of the Trochodendraceae. The morphological characters of *Zizyphoides flabella* are not entirely similar to modern members of the Trochodendraceae, as there are numerous morphological features intrinsic to this leaf type are absent from the modern, which indicates it may represent an early ancestor or archaic form (Crane et al. 1991). The associated infructescences, *Nordenskioeldia,* share some characteristics with modern members of the Trochodendraceae, but there are a numerous morphological differences (Crane et al. 1991), which appears to confirm the archaic nature of these Paleogene representatives.

The absence of *Nordenskioeldia* infructescences from the BTVP and the poorly constrained systematic position of AM11 with other *Zizyphoides* leaf types prevents an accurate association of this morphotype with a modern group, and is therefore tentatively associated with the Trochodendraceae.

3.19 Angiosperm morphotype 12 (AM12)

3.19.1 Specimen numbers

The specimen number of this morphotype is: AM.NA.106-c.

3.19.2 Diagnosis

Laminar size mesophyll, laminar shape unclear, blade symmetry unclear, unlobed, margin serrate. Apex and base not preserved. Primary venation pinnate, agrophic veins absent. Major secondary veins appear semicraspedodromous, interior secondary veins absent, minor secondary veins absent, major secondary vein spacing decreasing proximally, secondary vein angle inconsistent, major secondary attachment excurrent. Intersecondary veins absent. Intercostal tertiary veins unclear opposite percurrent or mixed percurrent. Epimedial tertiary veins appear opposite percurrent reticulate with proximal perpendicular to the midvein and distal course parallel to intercostal tertiary veins. Exterior tertiary vein course unclear possibly looped. Higher order venation not preserved. Tooth spacing, order and number of teeth/cm unknown. Tooth shape unclear appears convex/convex, sinus shape unclear. Principle vein present with termination at apex.

3.19.3 Identification

Angiosperm morphotype 12 (AM12) is represented by one poorly preserved specimen, the preservation of its venation has enabled it to be distinguished from other morphotypes from Skye. The pinnate semicraspedodromous venation pattern of this morphotype appears similar to AM6, but lacks the characteristic intersecondary veins of AM6 and its reticulate tertiary veins, which indicates it is a separate morphotype.

The limited preservation of this morphotype makes its identification to a known fossil taxon difficult, the absence of base, apex, low venation clarity and much of the margin limit its comparability. AM11 appears to be similar to two species of poorly preserved leaves from Svalbard, *Magnoliaephyllum* sp.1 and *Magnoliaephyllum* sp.2 (Budantsev and Golovneva 2009). It appears to have the same primary, secondary and tertiary venation characteristics but cannot be conclusively attributed to this enigmatic taxon, AM12 is therefore regarded as representing a woody dicotyledonous angiosperm with unknown affinity. Additional specimens that have the characteristics venation of AM12 are required to provide a more accurate assement of its systematic position. Comparisons with other fossil and modern taxa cannot therefore be made and so these sections are omitted for this morphotype.

3.19.4 Discussion

The single specimen of AM12 (AM.NA.106-c) (Figure 3.38) provides little information regarding its leaf form, the specimen appears to have been fragmented during transport or after it was deposited and part of the distal portion of lamina has broken away and been rotated. The specimen appears to relatively large leaves as it has a fragmented area of 3170mm^2, and based on the curvature of the venation it appears to have been mesophyll prior to its fragmentation. The shape of the leaf is unclear but the widest preserved sections are in the middle and upper portions of the laminar, which may indicate it was elliptic or obovate originally. The laminar length:width ratio of this morphotype is difficult to determine but is estimated to have been ~1.4:1.

The major secondary veins appear to be semicraspedodromous as they appear to form loops with the adjacent secondary veins and branch towards to the margin. Additional loops appear to be present exmedially and these appear to be formed by secondary and tertiary veins. Secondary vein angle appears to be inconsistent and ranges from 33 ° to 60 °. The tertiary venation is poorly preserved but the intercostal tertiary veins appear to be opposite percurrent or alternate percurrent, which may suggest the overall pattern is mixed percurrent.

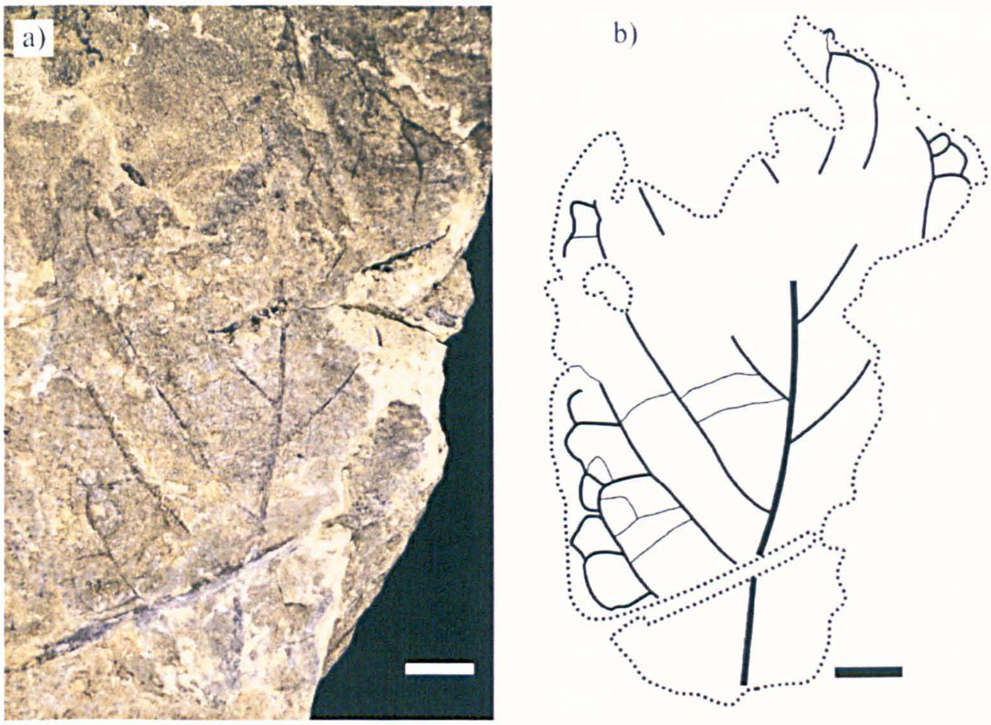

Figure 3.38. The single specimen of AM12. a) AM.NA.106-c, b) line drawing of AM.NA.106-c. Scale bars = 1 cm.

The margin is partially preserved in a small portion of the distal laminar and indicates that AM12 had a toothed margin, the tooth shape is unclear but both distal and proximal flanks appear convex. A principal vein supplies the tooth and terminates at the apex, it originates from a secondary vein loop but appears of narrower gauge and is considered to be a marginal tertiary vein.

3.20 Angiosperm morphotype 13 (AM13)

3.20.1 Specimen numbers

The specimen numbers of this morphotype are: AM.NA.061-d, 0082-d, 0163, AM.NA.0175-a, AM.NA.2008.004-c.

3.20.2 Diagnosis

Lamina size microphyll to meosphyll, length:width ratio unclear (possibly 1:1-1.5:1), shape appears elliptic and medially symmetric, base appears asymmetric (possible basal insertion), unlobed, margin serrate. Apex not persevered, base angle obtuse with a convex shape. Primary venation pinnate, naked base veins absent, one basal vein present, compound agrophic veins. Major secondary veins craspedodromous, interior secondary veins absent, minor seconsecondary angle increases smoothly to abruptly proximally, attachment proximally decurrent. Intercostal tertiary veins opposite percurrent with obtuse vein angle that increases exmedially. Epimedial tertiary veins opposite percurrent with proximal course parallel to intercostals tertiary veins or perpendicular to midvein and distal course parallel to intercostal tertiary veins. Higher order venation not preserved. Tooth spacing and number of orders unknown, sinus shape rounded. Tooth shapes convex/convex. Principal vein present and terminating at the tooth apex.

3.20.3 Identification

Angiosperm morphotype 13 (AM13) appears broadly similar to other pinnate craspedodromous leaf morphotypes of Skye such as AM3 and AM4. It can be distinguished from these leaf types, however, by the obtuse angle of its secondary and tertiary veins, the proximally decurrent attachment of its secondary veins and the asymmetric basal insertion. Although this morphotype can be distinguished from others from the Allt Mor assemblage it cannot be readily identified to other fossil taxa because of its limited preservation. Two leaf types from the Eocene of Svalbard appear to be broadly similar *Grewopsis* and *Ushia* as they have a similar basal form, secondary and tertiary veins and major secondary vein attachment as AM13 (Kvacek et al. 1994). It is difficult to distinguish *Grewopsis* and *Ushia* from each other unless they are nearly complete and well preserved (Clifton pers comm. 2010). The margin of these two leaf types is useful feature to distinguish them, but is of limited value for AM13 as only a small portion of lamina is preserved in one specimen.

The limited preservation of AM13 and its similarities to two other leaf types prevents an accurate assessment of this morphotypes identity and it is considered enigmatic. The collection of additional specimens of this leaf type may provide additional morphological information to confirm that it is related to either *Grewopsis* or *Ushia*. Due to the unresolved systematic position of AM13 sections pertaining to its similarities to fossil and modern taxa have been omitted.

3.20.4 Discussion

Specimens of AM13, although fragmented appear to have been originally large, estimations of their orginal lamina area up to 5000 mm^2 to 6000 mm^2, which suggests they were mesophyll prior to fragmentation (Figure 3.39 and 3.40). The basal morphology of this morphotype is partially understood as specimens (AM.NA.2008.004-c and AM.NA.061-d) have them partially preserved (Figure 3.39-a, c). The bases on both specimens appear to be asymmetric with a basal insertion, this feature appears to be most developed in specimen AM.NA.061-d.

The major secondary veins are a distinctive character of this morphotype with the proximally decurrent attachment, obtuse angle with a straight course. Secondary vein spacing is relatively uniform across the lamina but does show a slight decrease proximally. The angle of the secondary veins in the central portion of the lamina range from 33-50° but are most often 40-50°, proximally vein angles increase to 50 ° to 60°.

The intercostal tertiary veins are opposite percurrent with predominately convex course, although straight and sinuous courses do occur. The angle of the intercostals relative to the midvein is obtuse with admedial ranges of 100 ° to 125 ° and increase exmedially to 120 ° to 140 °. The epimedial tertiary veins are opposite percurrent and have proximal courses that are parallel to the intercostal veins or perpendicular to the midvein, the former being most common closer to the intersection between the subjacent secondary and the midvein. The distal course appears to be solely parallel to the intercostal veins.

The marginal characteristics of this morphotype are only known from the base of one specimen, AM.NA.061-d, which has a several partially preserved teeth. The flanks of the teeth are convex with longer proximal flanks. A principal vein is present and terminates at the margin. Accessory veins appear present and may be derived from the loops of the agrophic veins, but are too poorly preserved to determine definitely.

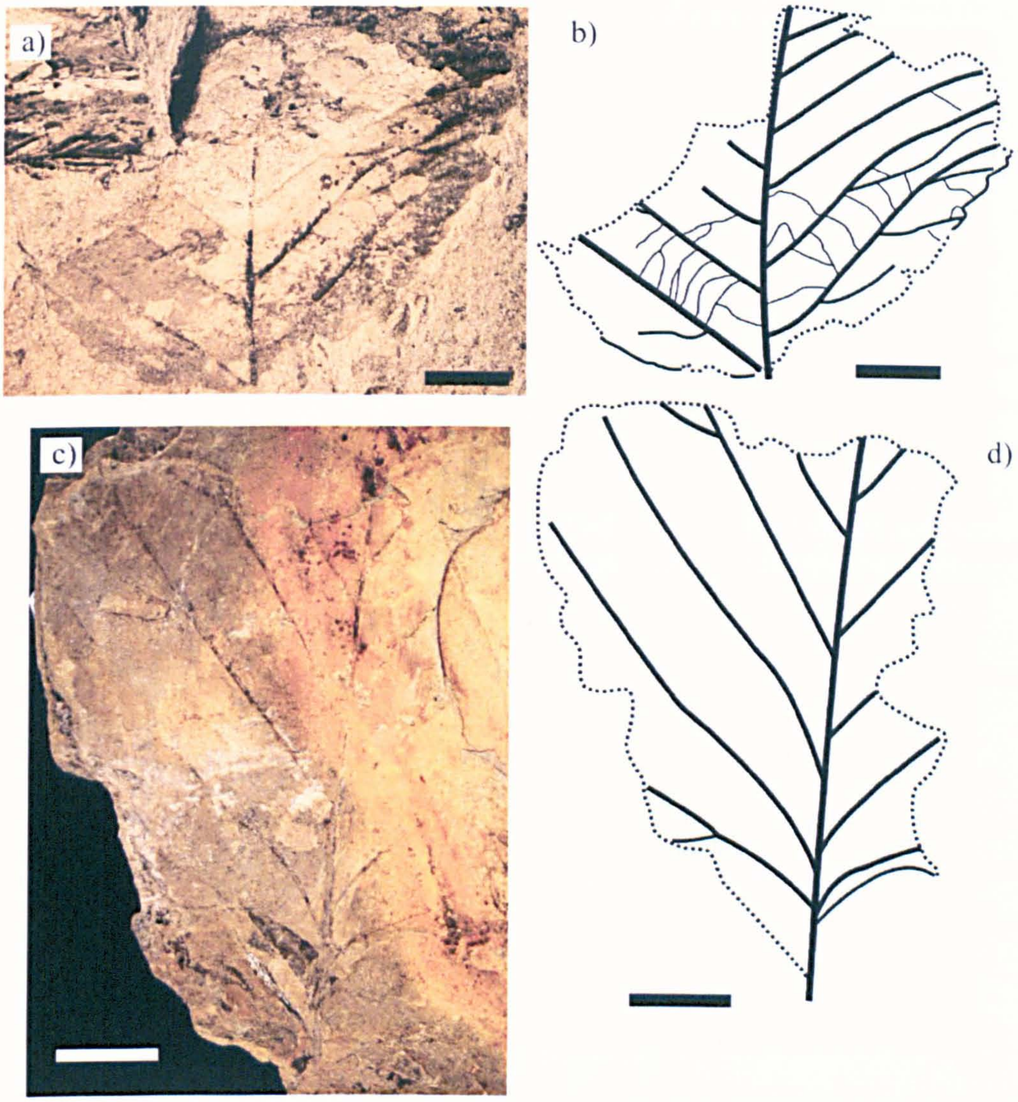

Figure 3.39. Specimens of AM13. a) AM.NA.2008.004-c, b) line drawing of AM.NA.2008.004-c, c) AM.NA.061-d, d) line drawing of AM.NA.2008.004-c. Scale bars =1cm.

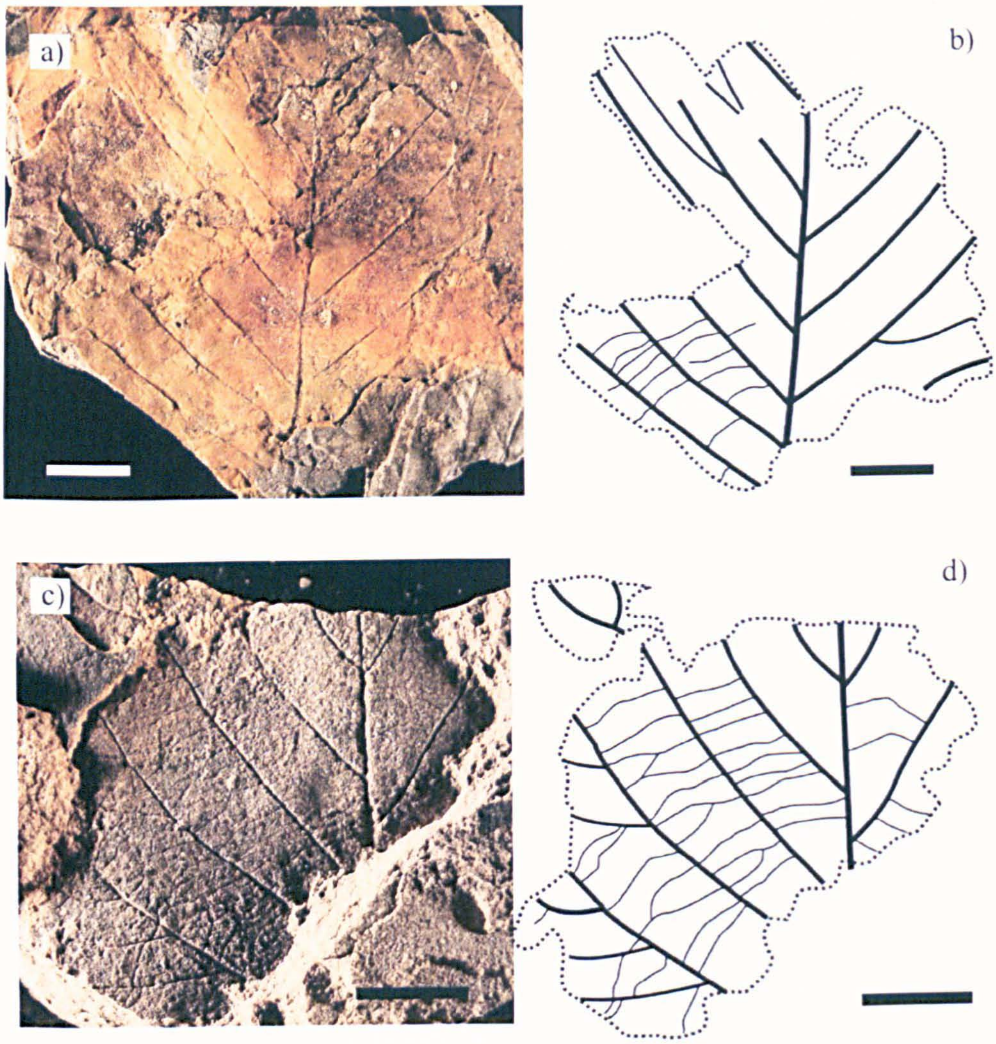

Figure 3.40. Specimens of AM13. a) AM.NA.175-a, b) line drawing of AM.NA.175-a, c) AM.NA.163, d) line drawing of AM.NA.175-a. Scale bar = 1 cm.

3.21 Angiosperm morphotype 14 (AM14)

3.21.1 Specimen numbers

The specimen number of this morphotype is: ACC.001-e.

3.21.2 Diagnosis

Blade attachment appears marginal, laminar size notophyll, laminar L:W ratio unclear, laminar shape appears elliptic, blade medially symmetrical, base appears symmertic, unlobed, margin unknown. Apex angle unknown, apex shape unknown, base angle obtuse, base shape appears concavo-convex. Primary pinnate, naked basal veins absent, five basal veins, agrophic absent. Major secondary veins appear scraspedodromous, interior secondary veins present, major secondary spacing abruptly decreasing proximally, secondary angle inconsistent, major secondary attachment decurrent. Intersecondary veins absent. Intercostal tertiary veins irregular reticulate. Epimedial tertiary veins reticulate. Quaternary vein fabric alternate percurrent. Aerolation development good, freely ending veinlets absent.

3.21.3 Identification

Angiosperm morphotype 14 (AM14) is represented by a single specimen that has excellent venation clarity with at least four vein orders preserved over much of the laminar. This morphotype is characterised by its prominent interior secondary veins that extended between the major secondary veins. The only other morphotype with such pronounced interior secondary veins is AM1 (*Platanites hebridicus*), but the leaves preserved in the Allt Mor assemblage are palinactinodromous and not pinnate like AM14. The lateral leaflets of *Platanites hebridicus* from Ardtun of Mull are pinnate but lack the interior secondary veins, which indicate AM14 is not a specimen of AM1.

Interior secondary veins are common in leaves that are lobed such as those in the Sapindaceae, particularly *Acer* (Ellis et al. 2009). The leaf specimen of this morphotype is too poorly preserved to determine if it is lobed, the secondary veins and interior veins connecting them indicate that if the leaf was lobed the sinuses were shallow. *Acer arcticum* from the Paleogene of Svalbard has similar interior secondary vein structure as AM14 (Budanstev and Golovneva 2009). This leaf type does differ significantly to AM14 as it has actinodromous primary veins, while AM14 is pinnate, which indicates it may not be related to the Sapindaceae.

The lack of marginal, basal or apex preservation limits the ability to identify this morphotype to a known fossil taxon despite of its excellent venation clarity. It is therefore regarded as woody dicotyledonous angiosperm of unknown affinity. Comparisons with other fossil and modern taxa cannot therefore be made and so these sections are omitted for this morphotype.

3.21.4 Discussion

As mentioned in the previous section AM14 is represented by one specimen (ACC. 001-e) that has very clear venation preserved, but little of its overall lamina form is discernable from the fragmented specimen (Figure 3.41). The fragmented laminar area of the specimen is 1410 mm², but the curvature and symmetry and symmetry of the laminar it appears it may have been > 2500 mm², suggesting it was notophyll prior to fragmentation. The laminar shape of AM14 is difficult to determine but appears it may have been elliptic, as the secondary veins in the central portion of the lamina have angles that are more obtuse and seem to extend further than those in the proximal and distal sections of the laminar.

The basal morphology of this morphotype is difficult to determine but a small portion of basal margin is preserved (Figure 3.41). The basal margin appears to have a concave curvature away from the midvein which may indicate this morphotype had a concavo-convex base shape.

The major secondary vein course of this morphotype is difficult to determine as points where they terminate are not preserved. The course of the secondary vein takes exmedially and the distance between the major secondaries suggests that these veins may have been craspedodromous and may have formed the principal vein for teeth. In section 3.21.3 it was suggested that AM14 may have been lobed as it has interior secondary veins, which are common in lobed leaf types (Ellis et al. 2009).

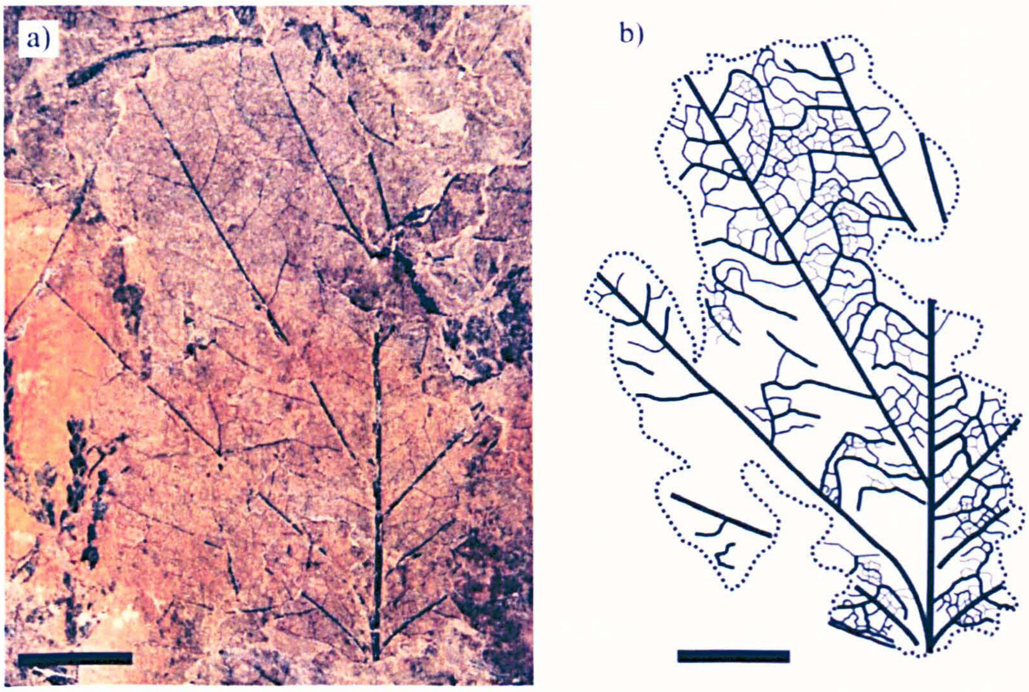

Figure 3.41. The single specimen of AM14. a) ACC.001-e, b) line drawing of ACC.001-e. Scale bars = 1 cm.

3.22 Summary

The fossil angiosperm leaves collected from the Skye plant assemblages are typically poorly preserved and are highly fragmented with low levels of venation clarity and limited margin, basal and apex preservation. Despite of these limitations enough well preserved specimens are present in the collection to identify and construct leaf morphotypes. In total 14 angiosperm leaf morphotypes have been recognised from the Allt Mor plant assemblage. The understanding of their overall leaf form and venation characteristics varies, many are well characterised by good specimens (e.g. AM1, AM2, AM3, AM4, AM6, AM8, AM9, AM10, AM11), while others are represented by a small proportion of poorly preserved specimens (e.g. AM7, AM12, AM13, AM14). Of the 14 morphotypes it was possible to identify 11 of them to previously described fossil taxa. The morphology of these related fossil taxa and the leaf morphotypes from Skye indicate that they share similarities to modern plant families, which include the Platanaceae (AM1), Cercidiphyllaceae (AM2), Betulaceae (AM3 and AM4), Fagaceae (AM5), Juglandaceae (AM6, AM7 and AM8), Vitaceae (AM9), Cornaceae (AM10) and the Trochodendraceae (AM11). The morphological Skye angiosperm leaf morphotypes and evidence from their relatives indicates that although these leaf types are related to modern representatives of these families they represent archaic, undifferentiated, or extinct forms.

The leaf morphotypes of Skye are similar to other fossil taxa from the Northern Hemisphere, which suggests there was floristic interchange between northern Britain and these other regions during the Paleocene. Some of the Skye angiosperm morphotypes appear to be related to common components of Northern Hemisphere species such as *Trochodendroides* (AM2), *Corylites* (AM3 and AM4), *Fagopsiphyllum* (AM5), *Cornophyllum* (AM10) and *Zizyphoides* (AM11). These plant genera appear to have been ecologically important components of Paleocene Arctic floras. Their presence in the BTVP, therefore, indicates that this flora is similar to that of the Arctic and vegetation was able to mix between these two regions during the Paleocene.

Not all of the angiosperm leaf morphotypes of Skye are similar to other Paleocene species from other Northern Hemisphere localities. Three leaf morphotypes that appear to represent members of the Juglandaceae are present in the Allt Mor flora, and appear to be distinct from other leaf types attributed to this family from the Paleocene. Juglandaceous pollen is both abundant and relatively diverse component of the palynomorph assemblages of Skye (Jolley 1997). The abundance and diversity of representatives of this family indicates that they may have been diversifying in this region during the mid Paleocene. One morphotype in particular, AM8 appears to be an early form of *Platycaraya*, and may represent one of the oldest records of this genus, and suggests that it may have originated in Europe.

Platanites hebridicus is a common element of the Skye leaf assemblages; this genus of the Platanaceae has only been previously described from Ardtun, Mull and the Ravenscrag Formation of Canada. This unusual distribution indicates that it must have migrated across the Arctic during the Early Paleocene, but appears to have only been successful in the BTVP during the mid Paleocene as it is absent from floras from Greenland and Svalbard.

The Skye angiosperms appear similar to other Northern Hemisphere floras from the Paleocene, but the presence of species that have only been recognised from the BTVP, suggests that it has its own distinct character.

Chapter 4: Conifer fossils of Skye

4.1 Introduction

Conifer shoots account for 55% of the fossil plant remains in the Allt Mor plant assemblage on Skye, which indicates that they were an important component of this flora during the mid Paleocene. This chapter presents the descriptions of the conifers from the Allt Mor plant assemblage of Skye. Three ovulate cone-types have been recognised along with eight shoot morphotypes, which indicates that the conifer component of the flora was relatively diverse. Currently Robert Mill from the Royal Botanical Gardens, Edinburgh is carrying out a detailed taxonomic study of the conifer fossils from Allt Mor. A comprehensive taxonomic study is therefore not suitable here, but their gross morphology and their identities are considered in order to understand their role in the Paleocene floras of Skye. All descriptions and comparisons with fossil and modern taxa presented here are from personal observations and measurements.

4.2 Differentiating the conifer fossils

4.2.1 Differentiating conifer ovulate cone types

There are two types of conifer fossils in the Allt Mor assemblage: ovulate cones and leafy shoots. Fossils of ovulate cones in the Allt Mor assemblage are relatively rare and often poorly preserved compressions or impressions of the external or internal anatomy. To differentiate the cone-types characteristics of their attachment to foliar material, their size and shape, scale orientation and cone scale features were considered. These characters were also used to determine their systematic position by comparing their morphology with modern relatives using Eckenwalder (2009) and Schulz et al. (2005).

4.2.1 Differentiating conifer shoot morphotypes

Conifer shoots are the most abundant element of the Allt Mor assemblage and indicate that a variety of conifer species inhabited Skye during the Paleocene. To differentiate the conifer shoots they were split into morphotypes in a similar manner as the angiosperm morphotypes, but instead of using leaf form and venation patterns to separate the specimens into morphotypes, leaflet shape was used. Three leaf shape categories were used to separate the conifer shoots and are 1) flattened needle-like, 2) scale-like and 3) needle-like. Individual conifer morphotypes were identified from these broader shape categories based on more detailed morphological features of the leaflet arrangement and structure. These morphological features were also used to determine their taxonomic affinities by comparing them with modern relatives using

Eckenwalder (2009). The morphological description of each conifer shoot morphotype and its taxonomic affinities are presented in sections 4.4.

4.3 Ovulate cone types of Allt Mor Skye

4.3.1 Ovulate cone type 1 (OC1)

Ovulate cone type 1 (OC1) are preserved as cross sections, so the interior of the cones is visible, but the external features are not preserved. The cones of OC1 are typically small, with widths ranging from 10 mm to 20mm, and a lengths of 15mm to 20mm, they are rounded to slightly oblong in shape (Figure 4.1). The dark colouration of the cones indicates that they are woody. One specimen (AM.NA.041-b) has a peduncle attached at its base, which is relatively short ~10mm and thin ~2mm. The peduncle of AM.NA.041-b appears to lack any attached leaflets (naked) except near the base where a small scale-like leaf is attached (Figure 4.1).

The internal structure of OC1 cones are characterised by their axis width, cone scale arrangement and an absence of a bract. The axis of OC1 cones is relatively broad (3 mm to 4mm) and is straight. The woody cone scales lack a distinct bract portion, which appears to be fused to the fertile cone scale (Figure 4.1). The cone scales have a thin profile as they diverge from the axis and expand abruptly near the outer margin of the cone, and become triangular or wedge shaped (Figure 4.1). The cone scales appear to be arranged in decussate whorls, those in the basal and upper sections are smaller and appear to be fused (Figure 4.1). The number of scales is difficult to determine because of limited preservation and the cross-sectional view of the cones, but there may have been 12 or more present originally. The outer appearance of the scales is difficult to determine but appears to have been indented in the centre. Seeds have not been preserved inside the cones.

The peduncle morphology, woody composition and arrangement of the cone scales indicate that the OC1 of Allt Mor may represent a Paleocene form of *Metasequoia*. This member of the Cupressaceae has woody ovulate cones that have a naked peduncle, except for several small scale leaves at its base (Figure 4.1), which appears very similar to AM.NA.041-b. *Metasequoia* also lacks a bract on the cone scale (typical of the Cupressaceae) and has a whorled decussate arrangement of its cone scales (Eckenwalder 2009) (Figure 4.1). Shoots attributed to *Metasequoia occidentalis* have been identified from Ardtun of Mull, which suggests it was present in the BTVP (Boulter and Kvacek 1989). Similar shoots have also been recognised at Allt Mor (conifer morphotype 1), which are discussed in section 4.4.1. The close morphological resemblance of OC1 with those of extant *Metasequoia* and the presence of its foliage in the BTVP indicates that this cone type is attributable to this extant genus, and is considered to be *Metasequoia occidentalis*.

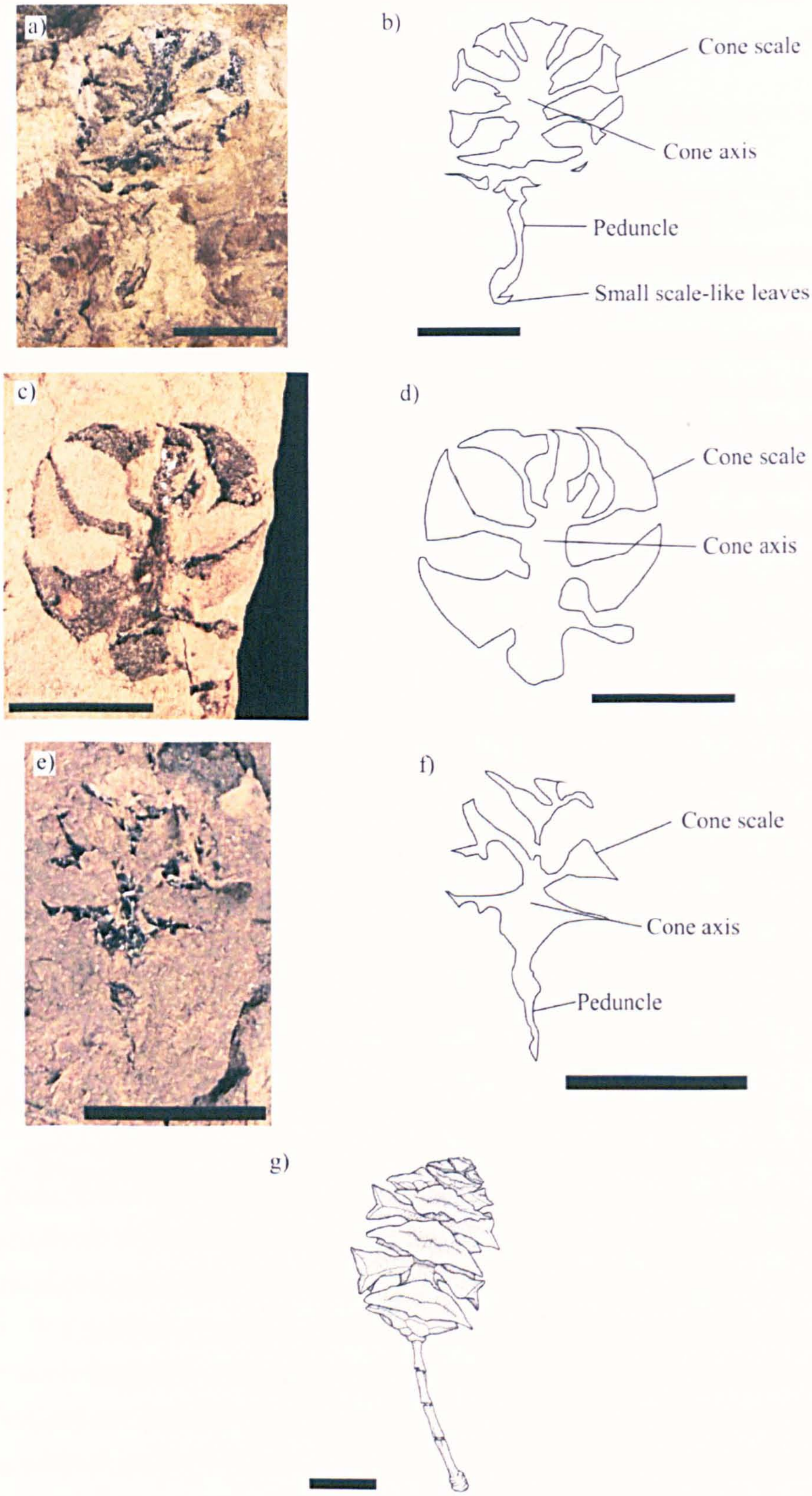

Figure 4.1. Examples of OC1. a) AM.NA.041-b, b) line drawing of AM.NA.041-b denoting morphological features, c) NMS.G.2004.29.076, d) line drawing of NMS.G.2004.29.076, e) AM.NA.169, f) line drawing of AM.NA.169 denoting morphological features, g) drawing of modern *Metasequoia* ovulate cone from Eckenwalder (2009). Scale bars =1 cm.

The second ovulate cone type (OC2) identified from the Allt Mor assemblage are poorly preserved and represented by two specimens (AM.NA.001-j, ACC.012-e) (Figure 4.2). The cones of OC2 appear similar to OC1 cones (*Metasequoia occidentalis*) except they are terminally attached to leafy shoots, which is uncharacteristic of *Metasequoia* (Chaney 1950, Schulz et al. 2005, Echenwalder 2009). The OC2 cones are preserved as compressions; the cones appear to be woody, have a rounded shape and are small ~10 mm long and ~15 mm wide (based on AM.NA.001-j). The better preserved of the two specimens (AM.NA.001-j) has partially preserved impressions of its cone scales, which appear to be decussate only in the basal section of the cone. The arrangement of the other cone scales is unclear but may be spirally (Figure 4.2).

The cones of both specimens of OC2 have a short 2mm to 3mm peduncle which are attached terminally to a leafy shoot. The shoot structure is better preserved in AM.NA.001-j and shows that the shoot bares flattened needle-like leaflets that appear spirally arranged around the axis. The leaflets are 3 mm to 5 mm in long and 0.5 mm to 1 mm wide, they have a prominent apex, which can be hooked or tapering (Figure 4.2). The leaflet arrangement of ACC.012-e near to its attachment to the cone is unclear but some of the leaflets preserved appear to have a similar arrangement to AM.NA.001-j. The arrangement of the leaflets on AM.NA.001-j appears to change further down its course, the leaves lower down the axis are decussate and alternate. These leaflets have a more rounded apex compared to those of AM.NA.001-j and are 5 mm to 10mm, the base of the leaflet appears to wrapped around the axis and there is no clear petiole.

The morphology of OC2, their attachment to a leafy shoots, and the leaflet form is characteristic of the Cupressaceae, and in particular members of the subfamilies Taxodioideae and Sequoioideae and (Eckenwalder 2009). Of the Taxodioideae subfamily the genus *Taxodium* appears to have similar shoot morphology, in particular the decussate leaflets of ACC.012-e, but its cones are not typically attached terminally to leafy shoots (Eckenwalder 2009). The cones of *Taxodium*, when mature are larger with diameters of 15 mm to 40 mm and the cones scales of this genus break away rapidly after they mature (Eckenwalder 2009). Fossil ovulate cones of *Taxodium* are typically rare, and are usually represented by disarticulated cone scales, which suggests the cones break apart like their modern relatives (Chaney 1950, Kunzmann et al. 2009). These differences indicate that OC2 is not a relative of *Taxodium*.

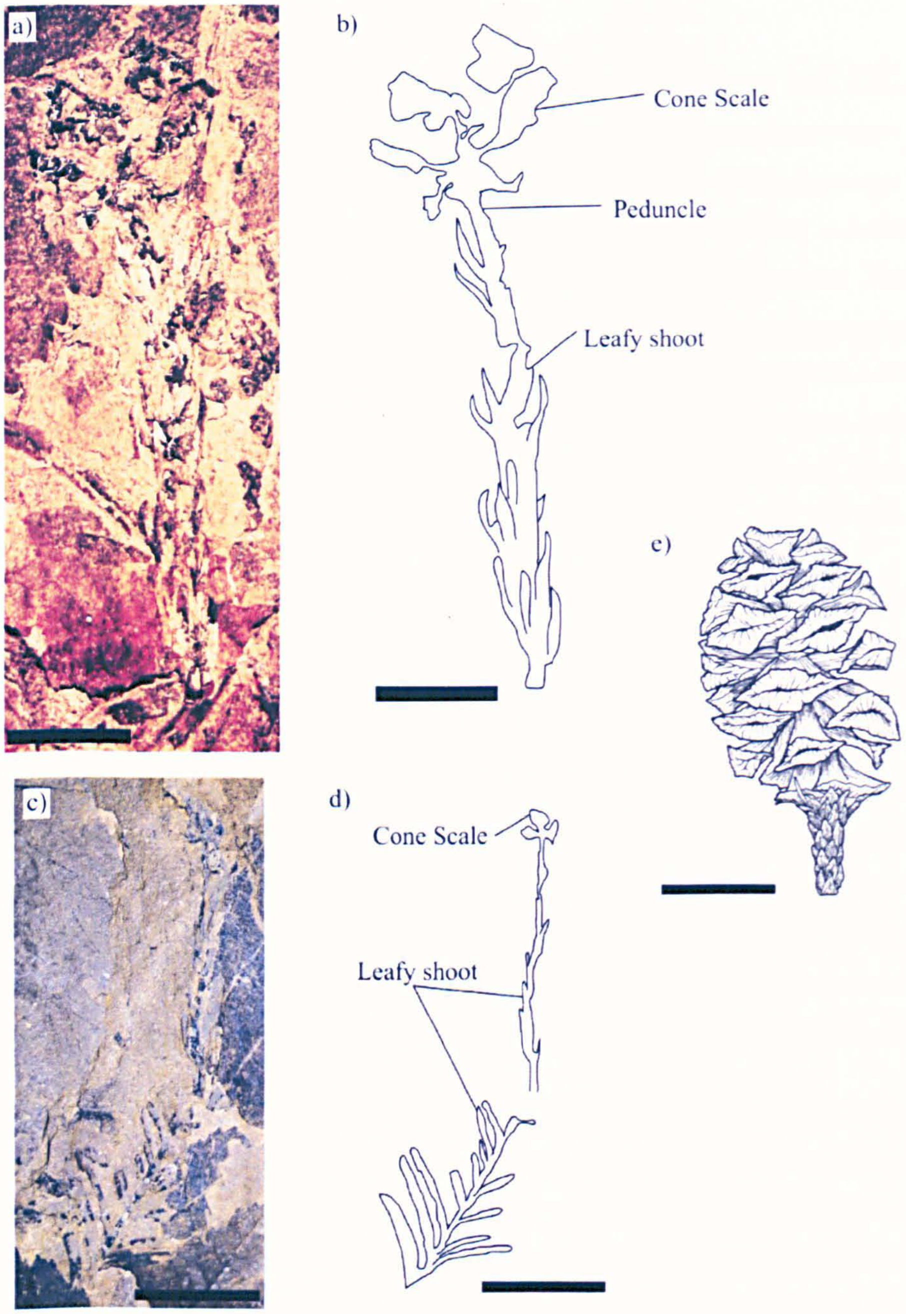

Figure 4.2. Examples of OC2. a) AM.NA.001-j, b) line drawing of AM.NA.001-j denoting morphological features, c) ACC.012-e, d) line drawing of ACC.012-e denoting morphological features, e) drawing of a modern *Sequoia* cone from Eckenwalder (2009). Scale bars =1 cm.

In the subfamily Sequoioideae two monotypic genera *Sequoiadendron* and *Sequoia* have ovulate cones and shoots similar to OC2 (Eckenwalder 2009). The ovulate cones of *Sequoiadendron giganteum* are considerably larger when mature with diameters of 15 to 30 mm, the leaflets of this species are more scale-like and more tightly arranged around the axis (Eckenwalder 2009), which suggests it is distinct from OC2.

Both in its ovulate cone form and shoot morphology OC2 is are remarkably similar to *Sequoia sempervirens* (Figure 4.2). The ovulate cones of *Sequoia sempervirens* are attached terminally to shoots that bare them, which is the same arrangement seen in OC2 (Eckenwalder 2009). The leaflets that develop from the cone bearing shoots in *Sequoia sempervirens* are different to OC2, they are smaller and more scale-like in form (Eckenwalder 2009). The leaflets that develop on sterile long and short shoots of *Sequoia sempervirens* are, however, very similar to those found on both specimens of OC2 (Eckenwalder 2009). This may indicate that the shoots of the Allt Mor form have retained the leaflets of the sterile shoots and have not developed the modified leaflets that *Sequoia sempervirens* has on its cone bearing shoots.

This assertion is partially confirmed by similar leaflet arrangement on ovulate cone bearing shoots of *Sequoia affins* from the Oligocene Florissant beds of Colorado. This Oligocene species of *Sequoia* is exceptionally well preserved, and has both staminate and ovualte cones attached to leafy shoots (Chaney 1950, McGinitie 1953). The leaflet arrangement and shape on shoots that bear ovulate cones in *Sequoia affins* are very similar to those of OC2 from Allt Mor. The leaflets of *Sequoia affins* have a flattened needle-like shape, blunt apexes and spirally or decussate arrangement around the axis (Chaney 1950, McGinitie 1953). The presence of this leaflet arrangement in another Paleogene form of *Sequoia*, suggests that modified leaflets seen on cone bearing shoots of modern *Sequoia* may be a more recent feature.

The similarity of the ovulate cones and leafy shoot structure of OC2 with both modern and Paleogene forms of *Sequoia* indicate that this ovulate cone type is a member of this genus. The differences in leaflet form on the ovulate cone bearing shoots of OC2 and modern *Sequoia sempervirens* indicates that this Paleocene representative may be a new species, and is therefore regarded as *Sequoia* sp.

4.3.3 Ovulate cone type 3 (OC3)

Two cones of OC3 have been identified and are attached to a shoot with scale-like leaflets (AM.NA.2009.030-d) (Figure 4.3). The two cones of OC3 are small 1 mm to 2 mm in length and ~1 mm in diameter. The small size of these cones may indicate that they are not fully mature, and have yet to develop into their maximum size. The ovulate cones of OC3 are attached to the shoot axis by relatively stout peduncles, the shoot axis appears to be devoid of leaf scales where these peduncles are attached.

The ovulate cones of OC3 are poorly preserved, but each shows different anatomical features, the lower cone appears to be an external compression or impression but shows some features of the external cone scale anatomy (Figure 4.3). The upper cone is preserved in cross section and shows features of the cone axis and the cone scales (Figure 4.3). The external cone anatomy of the lower cone is difficult to determine but there appear to be three scales in the central portion of the cone, the upper sections of the cone are unclear and the scales may be fused.

The cone scales in cross section are very thin where they meet the axis but expand abruptly at their periphery, where they form triangular scales (in cross section). The axis appears to relatively broad and approximately four times wider than the scales. The bract portion of the cone scale appears to be absent; its absence along with the attached shoot confirms its relationship to the Cupressaceae (Eckenwalder 2009).

The lowermost attached cone (Figure 4.3-c) is attached to the axis by a short but relatively broad peduncle. The shoot axis, to which the cone is attached, appears to be modified as it lacks any scale leaves for most of its course. This cone is preserved as an external compression or impression and shows little external or internal detail (Figure 4.3-c). The number and arrangement of the cone scales is unclear due to limited preservation but they appear to fused, which indicates they may be immature and have not opened to release the seeds.

The second cone is attached to an ultimate branchlet that has scale leaves. The second cone (Plate 4.3-c) is preserved as a cross section and shows some details of the internal structure of the cone. A short bract appears present on one of the cone scales but is greatly reduced to a small spur. Only two scales are preserved and appear to be very narrow laterally until they expand abruptly at the outer margin of the cone. In cross section the scales appear triangular in shape. The axis of the second cone appears to be relatively broad and is approximately four times thicker than the scales, the top of the axis may have several smaller or fused cone scales at its apex.

The limited preservation of the cones provides little systematic information of OC3, other than that it appears to be a member of the Cupressaceae. The attachment point of the cones peduncle on the shoot axis, and the morphology of the attached shoot indicate that it represents a species within the Cupressoideae subfamily, and is broadly similar to genera such as *Cupressus*, *Thuja* and *Chamaecyparis*. The attached shoot is poorly preserved but is comparable with conifer shoot morphotype 4 (CM4), these shoots have a characteristic morphology, which has enabled a clearer understanding of the systematic position of both plant organs, and is discussed in section 4.4.4.

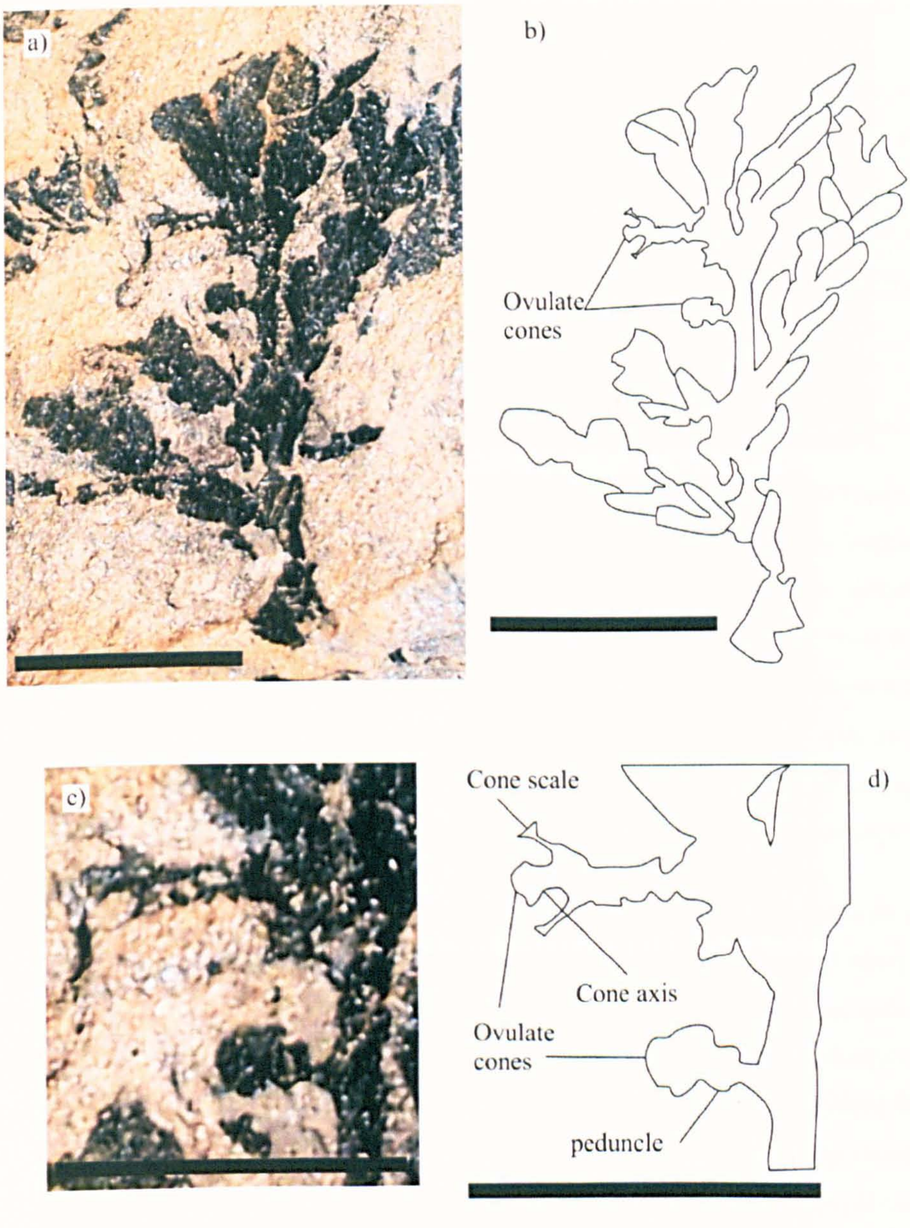

Figure 4.3. Example of OC3. a) AM.NA.2009.030-d, b) line drawing of AM.NA.2009.030-d denoting morphological features, c) close up of the two attached ovulate cones of AM.NA.2009.030-d, d) line drawing of the ovulate cones of AM.NA.2009.030-d denoting morphological features. Scale bars = 1 cm.

4.4 Conifer shoot morphotypes

The conifer shoot morphotypes from the Allt Mor assemblage were split into three shape categories, and where sorted into morphotypes based on more detailed features of their anatomy. Morphotypes in the flattened needle-like category are presented in sections 4.4.1 and 4.4.2, conifers with scale-like leaves are presented in sections 4.4.3 to 4.4.7 and one morphotype from the needle-like shape category is presented in 4.4.8.

4.4.1 Conifer shoot morphotype 1 (CM1)

Conifer shoot morphotype 1(CM1) is characterised by its decussate phyllotaxis (leaflets oppositely arranged in two flat rows) of its needle-like leaflets (Figure 4.4). The base of the leaflets are petiolate with a rounded shape, the apex is rounded or mucronate (Figure 4.4). The leaflet petiole is short and very slender and where it joins the leaf base it is twisted and decurrent. The individual leaflets width is variable, and ranges from 2 mm to 5 mm, the length of the leaflets are also variable and range and from 10 mm to 30 mm and have a prominent midvein (Figures 4.4). The angle of the leaflets relative to the axis is typically 45° to 60° but can be more acute with angles of 80° to 90°.

The distichous arrangement, where the two flattened rows of leaflets are oppositely arranged is unique to one genus in the Cupressaceae, *Metasequoia* (Chaney 1950, Eckenwalder 2009). The presence of ovulate cones characteristic of *Metasequoia* (OC1 see section 4.3.1) and shoots of *Metasequoia occidentalis* from the Ardtun leaf assemblage of Mull provide strong evidence that this species was present in the British Tertiary Volcanic Province (BTVP). It is likely therefore that the Skye forms represent the same species, and CM1 is regarded as *Metasequoia occidentalis*, and is associated with the ovulate cones of OC1 from Allt Mor.

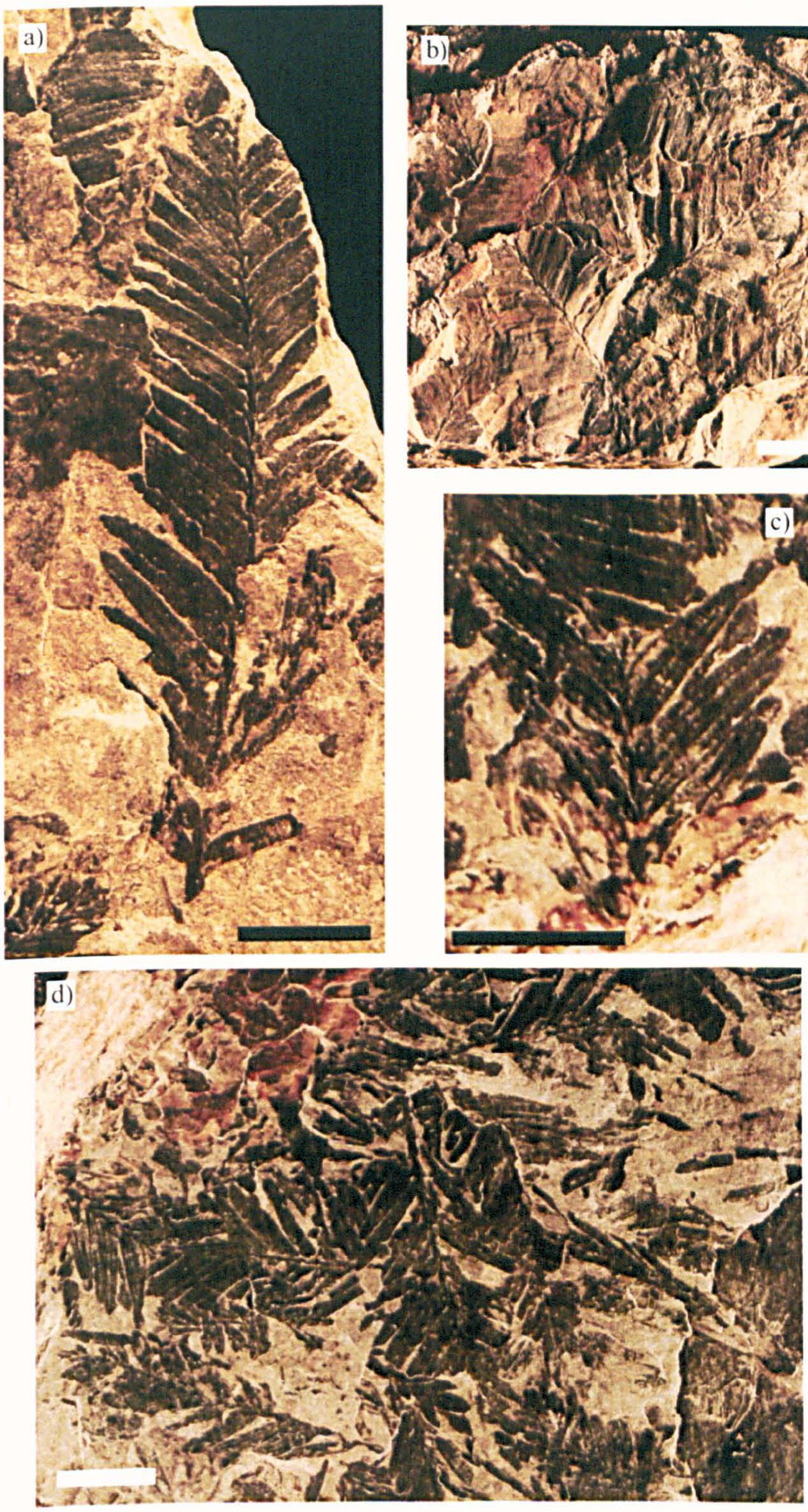

Figure 4.4. Examples of CM1. a) NMS.G.2004.29.008-a, b) NMS.G.2004.29.027, c) NMS.G.2004.29.008-b, high density of CM1 NMS.G.2004.29.008. Scale bars = 1 cm.

4.4.2 Conifer shoot morphotype 2 (CM2)

Shoots of conifer shoot morphotype 2 (CM2) are broadly similar to those of CM1 as the leaflets are flattened and needle-like and are arranged in pairs. The arrangement of the leaflet pairs is alternate and decussate (crisscross pairs) or slightly spirally and not truly distichous like CM1. This indicates that CM2 is not attributable to *Metasequoia*, but represents another conifer genus.

The flattened needle-like leaflets of CM2 are arranged on the axis in two ways, they are either spirally arranged around the axis and have a course that is perpendicular, or nearly so with the course of the axis, but more frequently the leaflets diverge from the axis with angles of 20° to 50° in decussate or spirally arranged alternate pairs (Figures 4.5 and 4.6). The base of the leaflets are wrapped around the axis and become partially distichously twisting of the leaflet base. The individual leaflets are 10 mm to 30 mm long and are 2 mm to 4 mm wide with apices that are typically obtuse, but may be acute. A single midvein is present in the centre of the leaflet but is often faint, possibly as a result of the relatively thick texture of the leaflets.

One specimen of CM2 and this specimens counterpart (NMSG.2002.64 and NMS.G.2004.29.100) have both long and short shoots preserved on the same specimen (Figure 4.5). The long shoot is only partially preserved but appears to have spirally arranged flattened needle-like leaflets attached to the long shoot axis, which diverge at angles of 10° to 20° from the shoot axis. The leaflets on the short shoots have a decussate arrangement and diverge from the axis at angles of 20° to 50°. The arrangement of the leaflets on the short shoots indicates that they may have been persistent (non-deciduous), as several growth increments are visible (Figure 4.6-a, b). It appears additional short shoots developed from the older shoots either terminally or laterally over successive growing seasons.

Conifer shoots similar to CM2 have been described from the Ardtun leaf assemblage of Mull. Boulter and Kvacek (1989) suggested that arrangement and shape of the leaflets on these shoots resembled *Sequoia*, but analysis of their cuticles indicated that they had affinities with *Taxodium*. Due to the conflicting evidence of their affinity Boulter and Kvacek (1989) assigned the shoots to the form genus *Elatocladus campbellii*, but suggested that this conifer may be more closely related to *Sequoia*. Ovulate conifer cones described in section 4.3.2 (OC2) were ascribed to *Sequoia* sp., the leafy shoots attached to these cones show significant similarities to CM2, which suggests that they may represent the same taxon. The leaflet form of CM2 is remarkably similar to both modern *Sequoia sempervirens* and the Allt Mor form, as they all have a sessile attachment to the axis, leaflet bases that do not narrow, an obtuse apex, similar divergence angles and a faint midvein (Chaney 1950). The combination of *Sequoia*-like cones (OC2) and shoots indicates that CM2 is a member of the genus, and is therefore regarded as *Sequoia* sp.

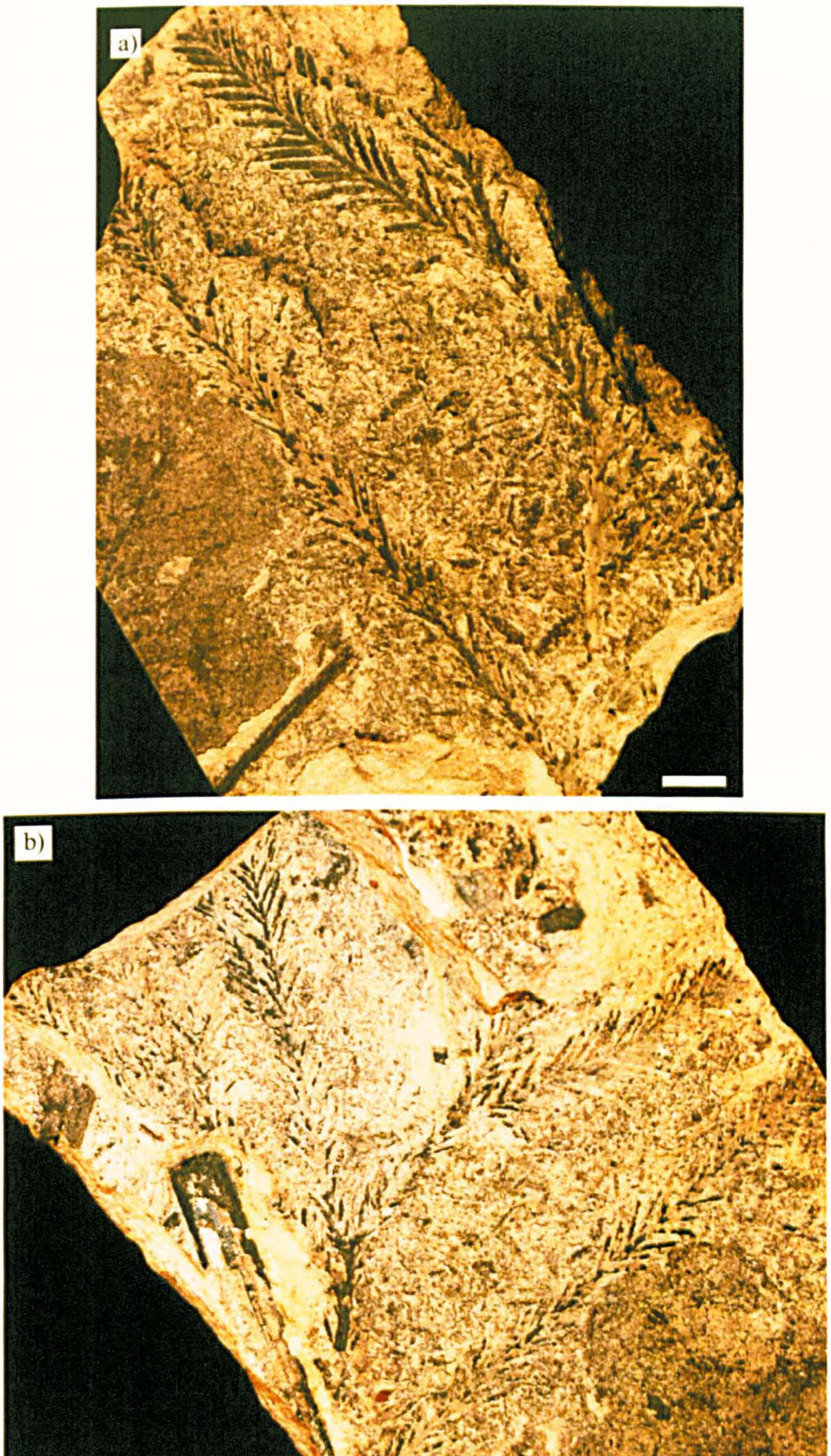

Figure 4.5. Examples of CM2. a) NMSG.2002.64, b) counterpart of NMS.G.2004.29.100. Scale bars 1 cm.

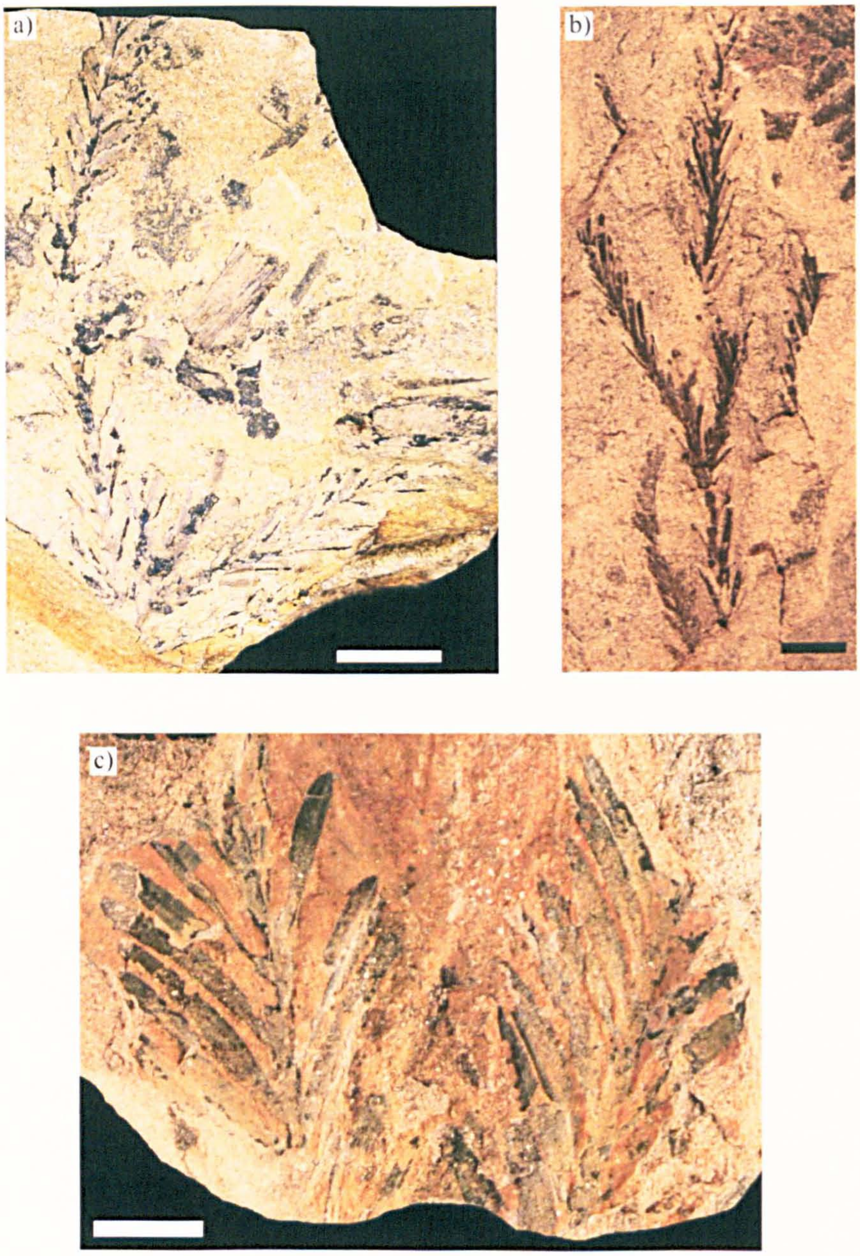

Figure 4.6. Examples of CM2. a) AM.NA.037, b) AM.NA.2008.002, c) NMS.G.2004.29.027. Scale bar = 1 cm.

4.4.3 Conifer shoot morphotype 3 (CM3)

Conifer morphotype 3 (CM3) is represented by short shoots that have both scale-like and claw-like leaflets that are spirally arranged around the axis of the stem (Figure 4.7). Conifer foliage with this configuration is often referred to as being cryptomerioid (*Cryptomeria*-like) (Ekenwalder 2009). Shoots of CM3 are often fairly short with lengths ranging from 30 mm to 50 mm, although longer shoots with lengths of >80 mm are present in the Allt Mor assemblage (Figure 4.7). Both claw-like and scale-like leaflets can be present on the same shoot, but claw-like leaflets are more common. The scale-like leaflets are most abundant and developed at the base of the shoot and become progressively more claw-like further up the shoot axis (Figure 4.7). The presence of claw-like leaves distinguishes CM3 from other conifer shoot morphotypes of the Allt Mor assemblage with scale-like leaflets (CM4 to CM7).

The cryptomerioid shoot form of CM3 is present in to several genera within the Cupressaceae including *Glyptostrobus*, *Taiwania* and *Cryptomeria* (Eckenwalder 2009). The foliage appears most similar to *Glyptostrobus* due the overlapping pattern of the scale-like leaflets and the size and shape of these leaflets is comparable. Shoots described as *Glyptostrobus dunoyeri* occur in Glenarm and Ballypaddy in Northern Ireland and Ardtun of Mull, which indicates that this genus was present in the BTVP during the Paleocene (Boulter and Kvacek 1989). The Skye forms have the same claw-like leaflets that are spirally arranged around the stem axis like those of described from other BTVP localities. This indicates that CM3 represents the same species, and is therefore regarded as *Glyptostrobus dunoyeri*.

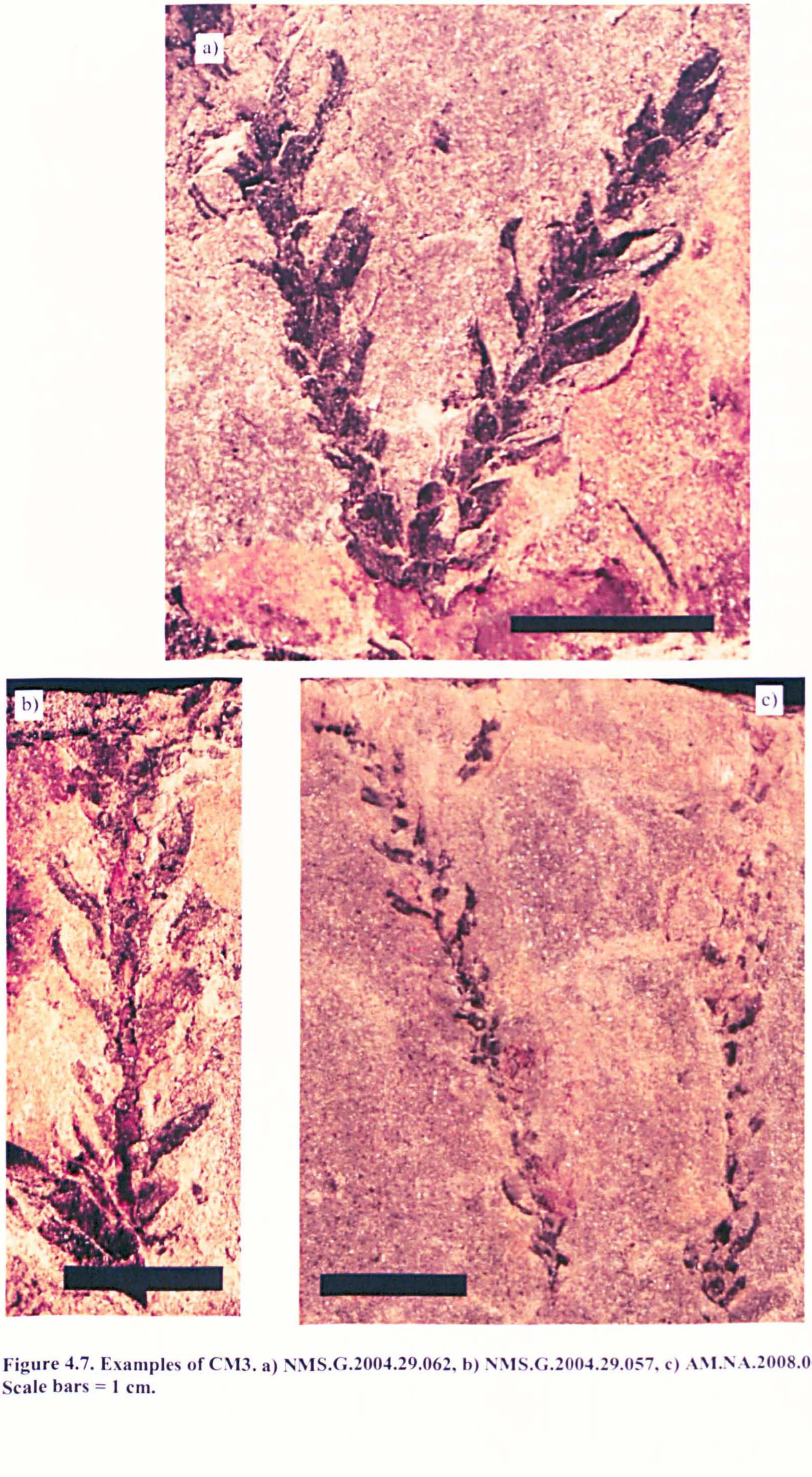

Figure 4.7. Examples of CM3. a) NMS.G.2004.29.062, b) NMS.G.2004.29.057, c) AM.NA.2008.009. Scale bars = 1 cm.

4.4.4 Conifer shoot morphotype 4 (CM4)

In section 4.3.3 ovualte cones (OC3) were described that were attached to a shoot (Figure 4.3) that appears to represent a member of the Cupressaceae in the subfamily Cupressoideae. The two attached ovulate cones of OC3 were too poorly preserved to determine their systematic position within the Cupressoideae. The shoot attached to the OC3 cones, and others similar shoots within the Allt Mor assemblage may provide additional information to improve the identification of this conifer.

The branchlets of conifer shoot morphotype 4 (CM4) appear to have been originally spirally arranged, as the compression of the individual branchlets is overlapping and does not appear to form sprays of branchlets (Figure 4.8). The leaflets on the branchlets are scale like and imbricate. The lateral leaflets are rounded and show little tapering, the apex is rounded and in some leaflets is slightly concave. The base of the facial leaflets are obscured by the laterals, as they intersect near their base. The facial leaflets appear to have a similar form to the lateral leaflets, suggesting the scales are monotypic (lateral and facial leaves same shape and size). The apex of the facial leaflets extends beyond the apexes of the adjacent lateral leaflets and joins the bases of the lateral leaflets above. The lateral leaflets on the major branchlets, or at the bifurcation of the minor branchlets have a different morphology. These laterals are longer, narrower and almost L-shaped in appearance, but in other respects are similar to the other lateral leaflets (Figure 4.8). One specimen (ACC.001-f), is well preserved and shows the arrangement and shape of leaflets clearly, as there contrast between the matrix and shoot impression (Figure 4.8-a).

The ovulate cones of OC3 associated to CM4 are too poorly preserved to provide a reliable identification of this conifers generic affinity. Comparisons with modern members of the Cupressoideae presented in Schulz et al. (2005), indicates that the shoot architecture of CM4 is comparable with the genus *Chamaecyparis*, and in particular *Chamaecyparis lawsoniana*.

The oldest known unequivocal representative of *Chamaecyparis*, *C. eureka* from the Middle Eocene deposits of the Buchanan Lake Formation of Axel Heiberg Island in the Canadian high Arctic (Kotyk et al 2003) is similar to CM4. The leaflet arrangement and shape of the CM4 and *C. eureka* is broadly similar, except that the Canadian specimens have conspicuous resin glands on the facial leaves, although this feature is not diagnostic of this genus (Schultz et al. 2005, Eckenwalder 2009).The attached ovulate cones and associated seeds of *C. eureka* are well preserved, which facilitated the accurate identification to the generic level. The ovulate cones of OC3 are too poorly preserved to make direct comparisons with *C. eureka*. The attachment of the ovulate cones to axis is perhaps the only comparable feature. The cones in *C. eureka* are attached to a leafy peduncle, this character is variable in the OC3 form as both leafy and naked peduncles are present.

The close morphological resemblance of the CM4 with that of modern and extinct members of the *Chamaecyparis* indicates that it may have a close affinity with this genus. The limited preservation of the attached cones prevents a reliable diagnosis, but what features are present indicates that the cones are different to any known members of *Chamaecyparis*. It is possible that this specimen is an archaic member of this genus, but cannot be confirmed with certainty, it is therefore considered as "*Chamaecyparis* cf.". If OC3 and its associated foliage CM4 are representatives of *Chamaecyparis* it could extend the fossil record of this genus to the mid Paleocene. A detailed examination of the cones and collection of more specimens is required to affirm this assertion.

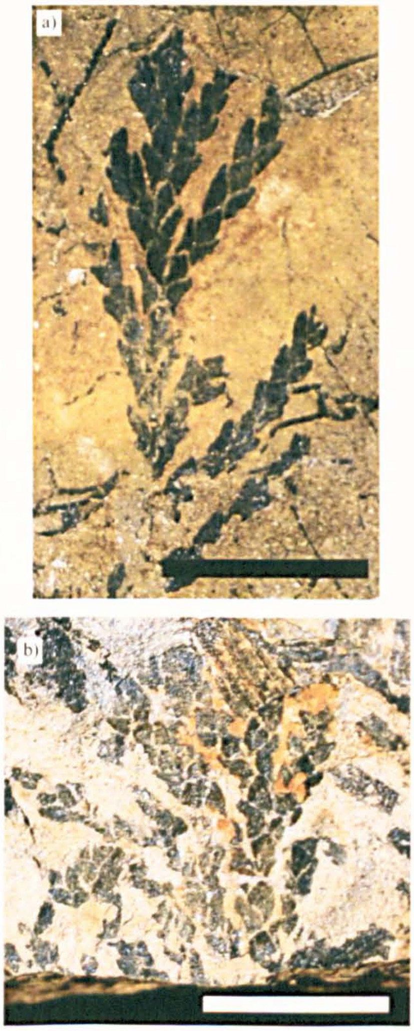

Figure 4.8. Examples of CM4. a) ACC.001-f, b) AM.NA.030-e. Scale bars =1 cm.

4.4.5 Conifer shoot morphotype 5 (CM5)

The leaflets of conifer shoot morphotype 5 (CM5) are scale-like and imbricate, the branchlets are distichous and alternate. The best preserved specimen of CM5 (ACC.003-d) (Figure 4.9-a), represents a well articulated shoot system with well preserved individual leaflets. The lateral leaflets are rounded with a blunt apex. The interior margin of the facial leaves can be straight or slightly concave, although the former is more common. The apex is blunt and well rounded or slightly convex. The lateral leaflets join at their base and are either partly or completely obscured basally by the proximal facial leaflet. The facial leaflets differ to the laterals in shape and form. The facials are shorter and almost diamond shaped and have a prominent ridge medially, while the lateral leaflets are more elongated with a rounded obtuse apex (Figure 4.9).

The alternate distichous arrangement of the branchlets and the shape of the facial and lateral leaflets separate this morphotype from the other cupressaceous foliage of the Allt Mor assemblage. The absence of attached cones or cuticle prevents a reliable identification of this morphotype. Comparisons with modern members of the Cupressoideae in Schulz et al. (2005) indicate that CM5 has a close affinity with the genus *Thuja*. The diamond shaped appearance of the facial leaves with their prominent medial ridge is consistent with the Allt Mor specimens (Figure 4.9). Despite of its close resemblance to *Thuja* it cannot be accurately demonstrated to represent this genus without further diagnostic information, such as cones or cuticle, and is therefore considered as "*Thuja* cf.".

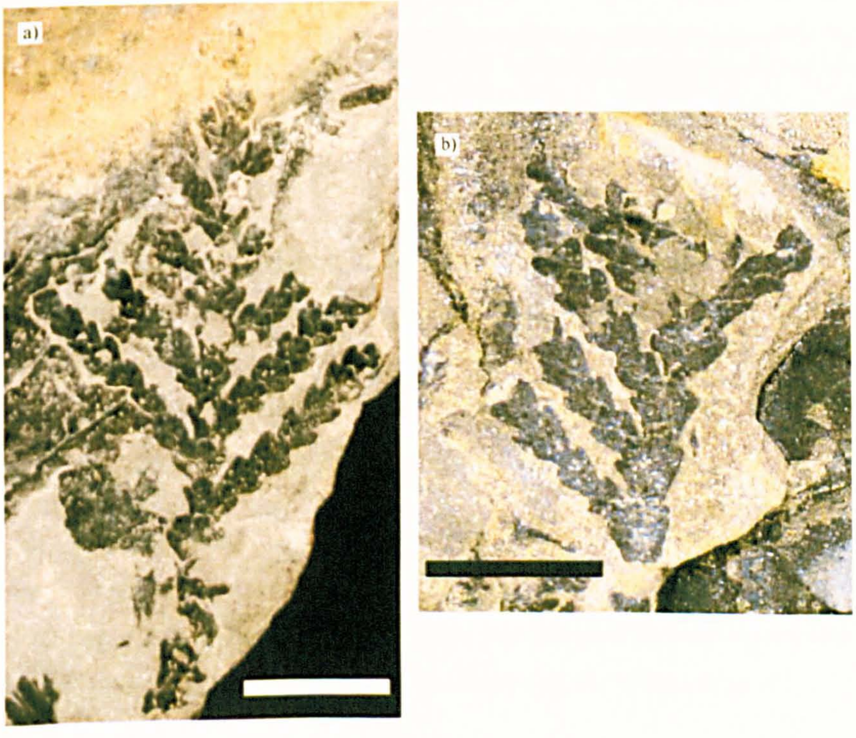

Figure 4.9. Examples of CM5. a) ACC.003-d, b) AM.NA.066. Scale bars = 1 cm.

4.4.6 Conifer shoot morphotype 6 (CM6)

The leaflets of conifer shoot morphotype 6 (CM6) are scale-like and imbricate, which indicates it represents another species associated with the Cupressoideae. This morphotype is represented by only two specimens (AM.NA.2008.013-e and NMS.G.2004.29.22) (Figure 4.10), but have features that distinguish them from other Cupressoideae morphotypes of Allt Mor. The lateral leaflets of CM6 are its most distinguishing feature, they have acute apexes, which can be straight or hooked in shape (Figure 4.10). The facial leaflets are poorly preserved but appear to be tapered at their base, they are straight sided and have an acute apex similar to the lateral leaflets. The lateral leaflets that develop where the branchlets bifurcate have a different appearance to the leaflets attached to the branchlets, as they are more widely splayed and are nearly L-shaped, with the apex directed ~90 ° to the branchlet axis (Figure 4.10-b).

Comparisons with modern members of the Cupressoideae described in Schultz et al. (2005) and Eckenwalder (2009) indicate that CM6 is unlike any modern member of this subfamily. An extinct member of this subfamily, *Mesocyparis* appears to be most comparable to CM6. Two species of *Mesocyparis* from the Late Cretaceous and Paleocene have been described from the Alberta and Saskatchewan of Canada respectively (McIver and Basinger 1987, McIver and Alenback 1994). Both of these species resemble CM6 in the overall morphology of the leaflets, but the Canadian forms are more complete and have attached cones. The lateral leaflets are highly similar in shape to CM6, and have the same prominent pointed or hooked apex. The laterals at the bifurcation points of the branchlets are similar those of CM6. It is likely that CM6 represents a species of *Mesocyparis*, and is therefore regarded as *Mesocyparis* sp.

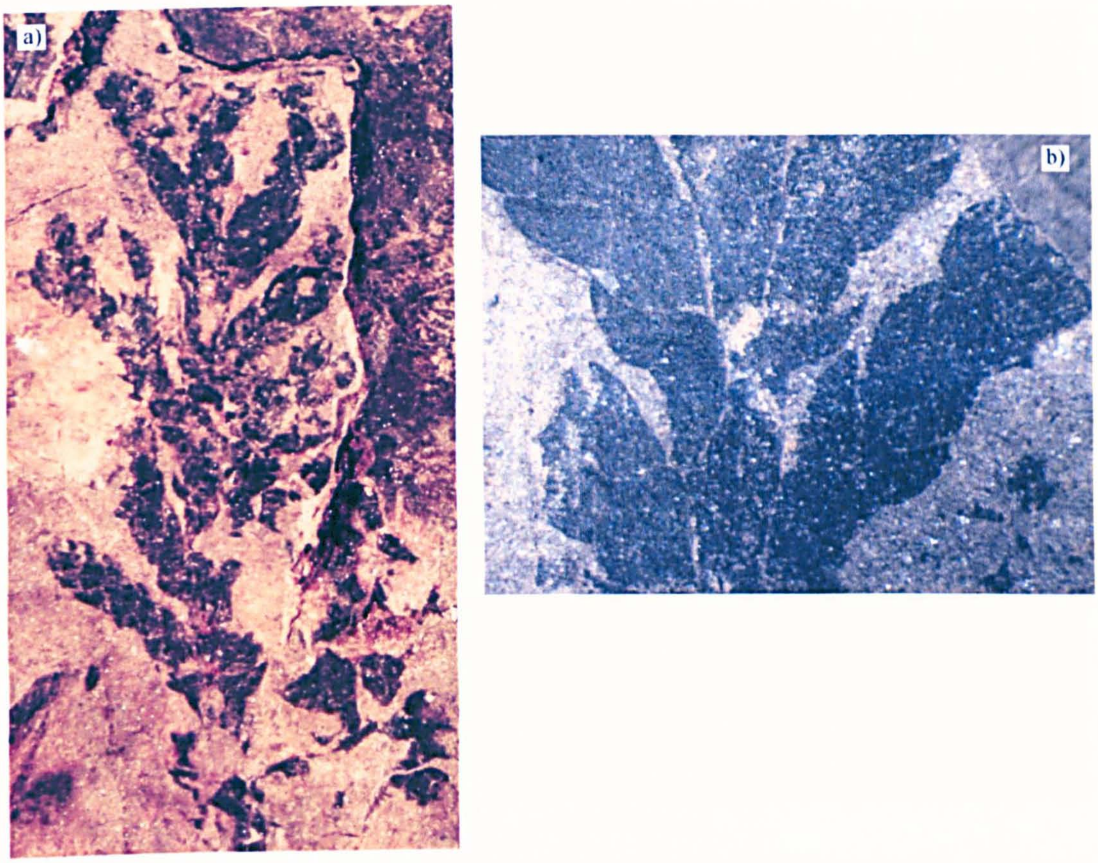

Figure 4.10. Examples of CM6. a) AM.NA.2008.013-e, b) NMS.G.2004.29.22, image supplied by Robert Mill. Scale bars = 1 cm.

4.4.7 Conifer shoot morphotype 7 (CM7)

Conifer shoot morphotype 7 (CM7) is based on a single poorly preserved specimen (NMS.G.2004.29.024-e) (Figure 4.11), it has scale-like leaflets that are imbricate, which indicates that it is a member of the Cupressoideae. This morphotype is distinguished from the other Cupressoideae morphotypes of Allt Mor by its greatly elongated facial and lateral leaflets and their apex morphology. Both the lateral and facial leaflets are rectangular in shape and are of a similar size, which indicates that they are monotypic. The apex of both facial and laterals are splayed away from the axis, and narrow towards the tip. The length of the leaflets gradually decreases distally, with the distal most scales being approximately a quarter the length of the proximal most scales.

The arrangement and shape of the facial and lateral leaflets indicates that CM7 may be attributable to *Calocedrus*, which has the same rectangular elongated leaflets (Eckenwalder 2009). The single specimen of CM7 is too poorly preserved and incomplete to determine its affinity confidently, and is therefore considered to be "*Calocedrus* cf.".

Figure 4.11. Example of CM7. NMS.G.2004.29.024-e image supplied by Robert Mill. Scale bar = 1 cm.

4.4.8 Conifer shoot morphotype 8 (CM8)

Conifer shoot morphotype 8 (CM8) is unique to the Allt Mor assemblage as it has needle-like leaves, which are characteristic of the Pinaceae (Eckenwalder 2009) (Figure 4.12). The needles are approximately 40 mm to 50 mm in length and have a width <3 mm. The needles have broad base and taper proximally and retain a relatively constant diameter for much of their length. The needles apex is often absent or poorly preserved, but appears to rounded and relatively blunt. The texture and external structure of the needles are poorly preserved but appears to be slightly striated.

The needles are too poorly preserved and disarticulated to ascribe confidently to a particular genus with the Pinaceae. Similar needles have been described from Northern Ireland and Mull and were attributed to *Pinus plutonis* (Boulter and Kvacek 1989). This may suggest that the Allt Mor needles may represent a form of *Pinus*, but due to the limited preservation they will be tentatively associated to this genus.

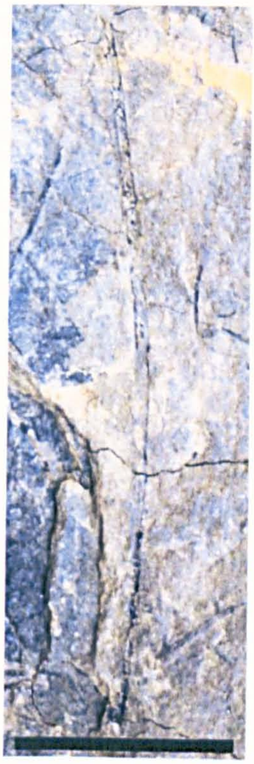

Figure 4.12. An example of CM8. AM.NA.078. Scale bar = 1cm.

The preliminary descriptive and taxonomic review of the Allt Mor conifers of Skye in this study indicates that they were both abundant and relatively diverse components of the flora. Three ovulate cone types have been identified and these show to similarities to *Metasequoia* (OC1), *Sequoia* (OC2) and *Chamaecyparis* (OC3). Eight conifer shoot morphotypes were identified and indicate that the conifers of Allt Mor are attributable to the families Cupressaceae and Pinaceae. The cupressaceous conifers are the most diverse conifer element, with all three ovulate cone types and seven of the shoot morphotypes attributed to this family. The seven shoot morphotypes represent three subfamilies within the Cupressaceae: the Sequoioideae, Taxodioideae and the Cupressoideae.

Two shoot morphotypes are attributed to genera within the Sequoioideae, CM1 and CM2. These shoot morphotypes appear similar to *Metasequoia* (CM1) and *Sequoia* (CM2) and are attributed to ovulate cone types OC1 and OC2 respectively. The presence of both cones and abundant leafy shoots of these genera provides strong evidence for their occurrence on Skye during the Paleocene. Conifer shoots that appear similar to CM2 (*Sequoia* sp.) have been identified from Ardtun of Mull, and were described as *Elatocladus campbellii* (Boulter and Kvacek 1989). The identity of this conifer was uncertain, but the confirmation that *Sequoia* was present in the BTVP suggests that the Mull form may be attributed to this genus, and this was a common conifer of the BTVP. The single representative of the Taxodioideae, CM3 appears similar to

Glyptostrobus dunoyeri of Northern Ireland and Mull. The presence of this conifer across the BTVP suggests that it was an abundant component of the flora.

The Cupressoideae subfamily is represented by four conifer shoot morphotypes and one ovulate cone type. The shoot morphotypes are tentatively associated to four genera, *Chamaecyparis* (CM4), *Thuja* (CM5), *Mesocyparis* (CM6) and *Calocedrus* (CM7). One specimen of CM4 has attached cones (OC3), these cones are poorly preserved but their association with the leafy shoot indicates that it represents a form of *Chamaecyparis*. If this association is correct it could represent one of the oldest records of this genus.

The Pinaceae are represented by one shoot morphotype (CM8), the needle-like leaves of this morphotype are characteristic of this family, but are too poorly preserved to establish their generic affinity. Similar needles attributed to *Pinus* have been described from Northern Ireland (Boulter and Kvacek 1989), but it is currently unclear if the Skye form is related.

The abundance and diversity of conifers in the Allt Mor flora indicates that this environment provided ideal growing conditions during the Paleocene. Continued work by Robert Mill of the Royal Botanical Gardens, Edinburgh may provide additional insights into these conifers and why they were so diverse on Skye during the Paleocene.

Chapter 5: Composition and vegetation structure of the fossil floras of Skye

5.1 Introduction

In this chapter the composition of the mid Paleocene vegetation of Skye is reconstructed. The relative abundance of each angiosperm and conifer morphotype is used to determine their ecological importance in the assemblages and to determine their growth habits. The taphonomy of the macrofossil assemblages of Skye are considered to determine its role in shaping of the plant assmebalges, and how the orginal vegetation compostion can be deciphered from the plant assemblages of Skye. The macrofossil record is compared to the palynomorph records from the Skye Lava Group to determine the more regional vegetation. These lines of evidence are used to reconstruct the vegetation of the macrofossil assemblages of Allt Mor, Allt Geodh' a' Ghamhna and Glen Osdale and the more regional vegetation of Skye during the mid Paleocene.

5.2 Floral composition and abundance of the Skye macrofossils

5.2.1 Floral diversity of Skye

The plant macrofossils recovered from the interbasaltic sequences from Allt Geodh' a' Ghamhna, Allt Mor and Glen Osdale have yielded a angiosperm and conifer flora. To date, 14 angiosperm leaf morphotypes, three ovulate cone species and eight conifer shoot morphotypes have been recognised and described in Chapters 3 and 4. The Allt Mor assemblage has provided the richest and best preserved fossil plant remains collected from Skye. Estimating the floral diversity of Skye from the plant macrofossils is therefore biased towards the Allt Mor assemblage. The Allt Geodh' a' Ghamhna and Glen Osdale collections are limited and poorly preserved, and both contain only fossils of broadleaf angiosperms.

The broadleaved angiosperm morphotypes recognised from the plant assemblages from the Skye Lava Group indicate that at least 14 angiosperm taxa were present in this region during the Paleocene (Figures 5.1, 5.2, 5.3). The affinities of many of these angiosperms have been determined by comparing their morphology with both fossil and modern taxa (Chapter 3). The morphotypes indicate that nine angiosperm families were present in Skye during the Paleocene (Table 5.1). The leaves are associated with the following families: Platanaceae, Cercidiphyllaceae, Betulaceae, Fagaceae, Juglandaceae, Vitaceae, Cornaceae and the Trochodendraceae. The majority of these families are represented by a single morphotype, except for the Juglandaceae, which has three morphotypes associated to it. However, the generic affinities of the angiosperm morphotypes cannot be determined with certainty as no reproductive structures have been found associated with the leaves.

Table 5.1. Fossil angiosperm morphotypes from Skye, showing their family affinity, described fossil species and localities from which they have been recorded.

Morphotype number	Family affinity	Described fossil species	Localities present
AM1	Platanaceae	*Platanites hebridicus*	AM, GO
AM2	Cercidiphyllaceae	*Trochodendroides antiqua*	AM, GO
AM3	Betulaceae	*Corylites hebridicus*	AM, AG, GO
AM4	Betulaceae?	*"Corylites cf."*	AM
AM5	Fagaceae	*Fagopsiphyllum groenlandica*	AM
AM6	Juglandaceae	*Juglandiphyllites sp.1*	AM
AM7	Juglandaceae	*Juglandiphyllites sp.2*	AM
AM8	Juglandaceae	*"Platycarya cf"*	AM
AM9	Vitaceae	*Vitiphyllum sewardii*	AM
AM10	Cornaceae	*Cornophyllum hebridicum*	AM, AG, GO
AM11	Trochodendraceae	*Zizyphoides sp.*	AM
AM12	unknown	unknown	AM
AM13	unknown	unknown	AM, GO
AM 14	unknown	unknown	AM

Locality codes; AM, Allt Mor; AG, Allt Geodh' a' Ghamhna; GO, Glen Osdale. AM1, AM2 etc. = angiosperm morphotype.

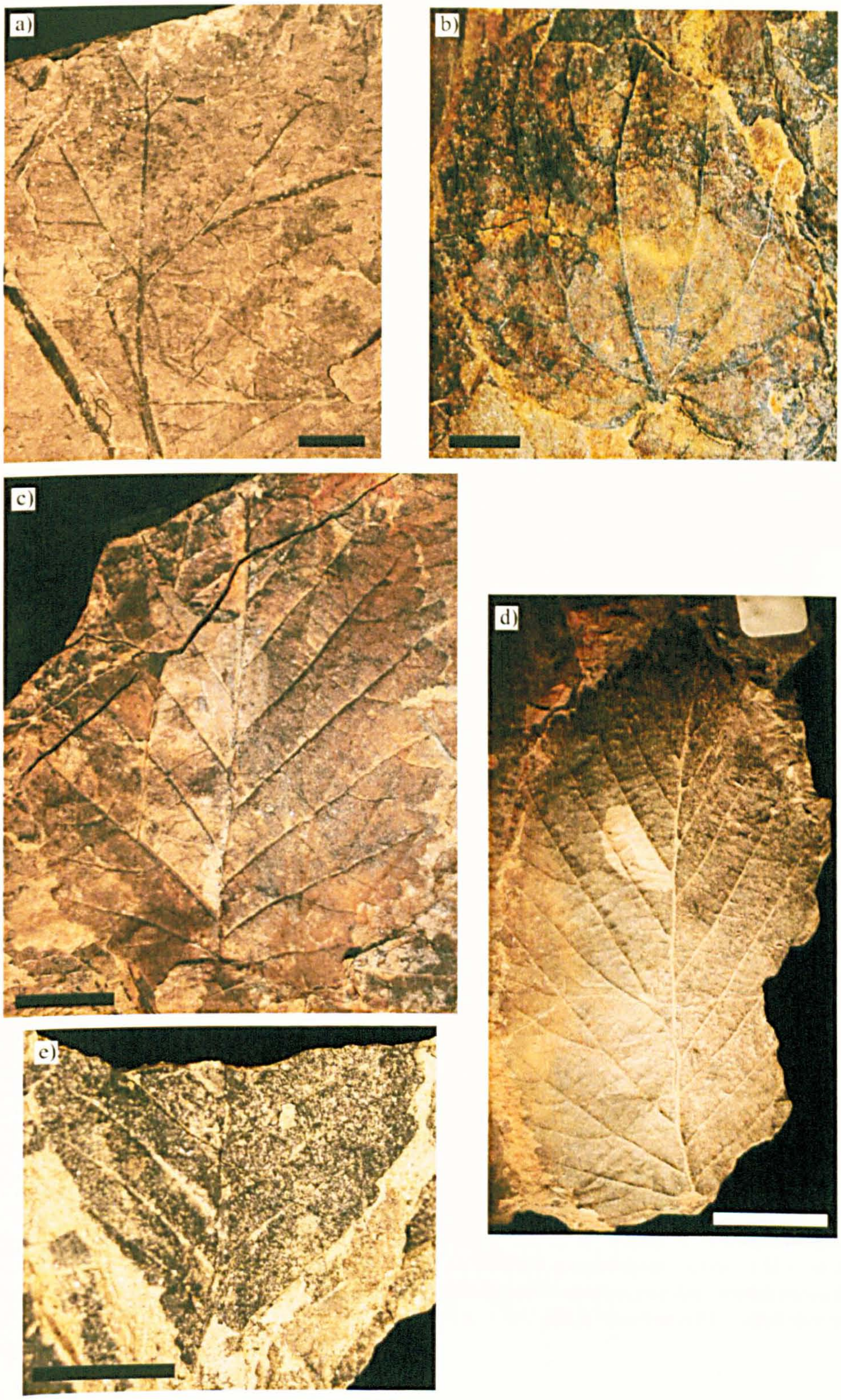

Figure 5.1. Representatives of angiosperm morphotypes 1 to 5. a) AM1 *Platanites hebridicus* (ACC.001-c), b) AM2 *Trochodendroides antiqua* (NMS.G.2004.29.47-a), c) AM3 *Corylites hebridicus* (ACC.012-b), d) AM4 "*Corylites* cf." (AM.NA.061-a), e) AM5 *Fagopsiphyllum groenlandica* (ACC.004-c). Scale bars =1 cm.

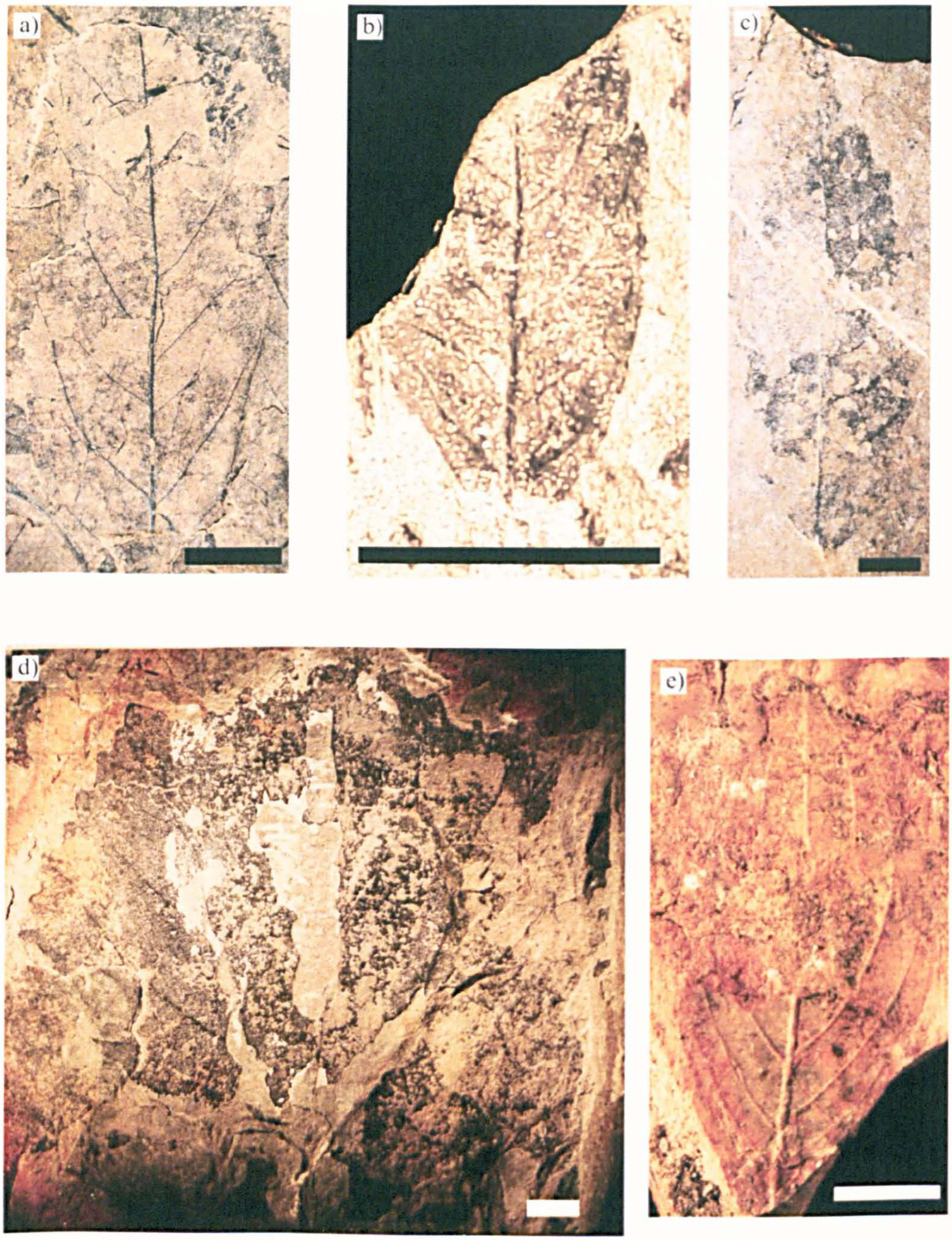

Figure 5.2. Representatives of angiosperm morphotypes 6 to 10. a) AM6 *Juglandiphyllites* sp.1 (ACC.001-b), b) AM7 *Juglandiphyllites* sp.2 (NMS.G.2004.29.008-a), c) AM8 "*Platycarya* cf." (AM.NA.184-a), d) AM9 *Vitiphyllum sewardii* (AM.NA.059-a), e) AM10 *Cornophyllum hebridicum* (NMS.G.2005.145.013-b). Scale bars =1 cm.

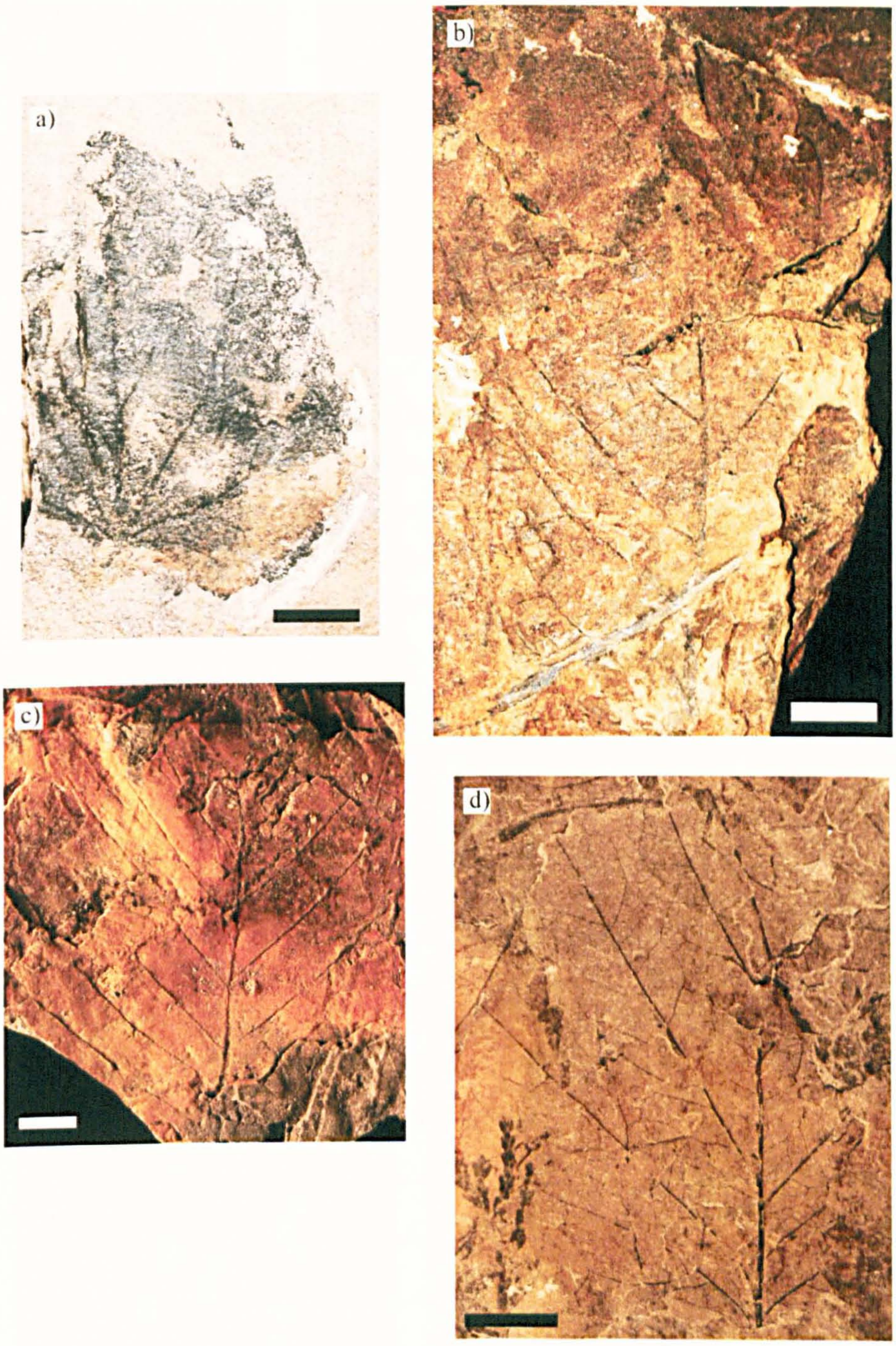

Figure 5.3. Representatives of angiosperm morphotypes 11 to15. a) AM11 *Zizyphoides flabella* (AM.NA.173-a), b) AM12 (AM.NA.106-c) c) AM13 (AM.NA.175-a), d) AM14 (ACC.001-e). Scale bars =1 cm.

Conifer macrofossils have been recovered only from the Allt Mor locality but are diverse and abundant components of the flora. The conifer fossils comprise three ovulate cone types and eight shoot morphotypes (Figure 5.4, Table 5.2). Comparisons with fossil and modern conifer taxa indicate that eight distinct species of conifer were present at Allt Mor during the Paleocene. These fossils show that two conifer families were present and include members of the Pinaceae and the Cupressaceae. Disarticulated needles associated with the Pinaceae were identified from the Allt Mor assemblage, but were too poorly preserved to establish their generic affinity and were placed into conifer morphotype 8 (CM8).

Macrofossils attributed to the Cupressaceae are the most diverse conifer component of the Allt Mor assemblage and are associated with three subfamilies: Sequoioideae, Taxodioideae and the Cupressoideae. Two ovulate cones (OC1 and OC2) and two associated shoot morphotypes (CM1 and CM2) were identified as representatives of the Sequoioideae and include *Metasequoia occidentalis* and *Sequoia* sp. The Taxodioideae is represented by a single shoot morphotype (CM3), which is attributed to *Glyptostrobus dunoyeri*. Macrofossils associated with the Cupressoideae are the most diverse element of the cupressaceous fossils and include four morphotypes that are tentatively associated with *Chamaecyparis* (CM4), *Thuja* (CM5), *Mesocyparis* (CM6) and *Calocedrus* (CM7).

Table 5.2. Conifer ovulate cone and shoot morphotypes from Allt Mor, with their family and subfamily affinities and associated fossil taxa.

Morphotype number	Family affinity	Subfamily affinity	Associated taxa
OC1	Cupressaceae	Sequoioideae	*Metasequoia occidentalis*
OC2	Cupressaceae	Sequoioideae	*Sequoia sp.*
OC3	Cupressaceae	Sequoioideae	*Metasequoia occidentalis*
CM2	Cupressaceae	Sequoioideae	*Sequoia sp.*
CM3	Cupressaceae	Taxodioideae	*Glyptostrobus dunoyeri*
CM4	Cupressaceae	Cupressoideae	"*Chamaecyparis* cf."
CM5	Cupressaceae	Cupressoideae	"*Thuja* cf."
CM6	Cupressaceae	Cupressoideae	*Mesocyparis sp.*
CM7	Cupressaceae	Cupressoideae	"*Calocedrus* cf."
CM8	Pinaceae	unknown	unknown

OC = ovulate cone type, CM = conifer shoot morphotype.

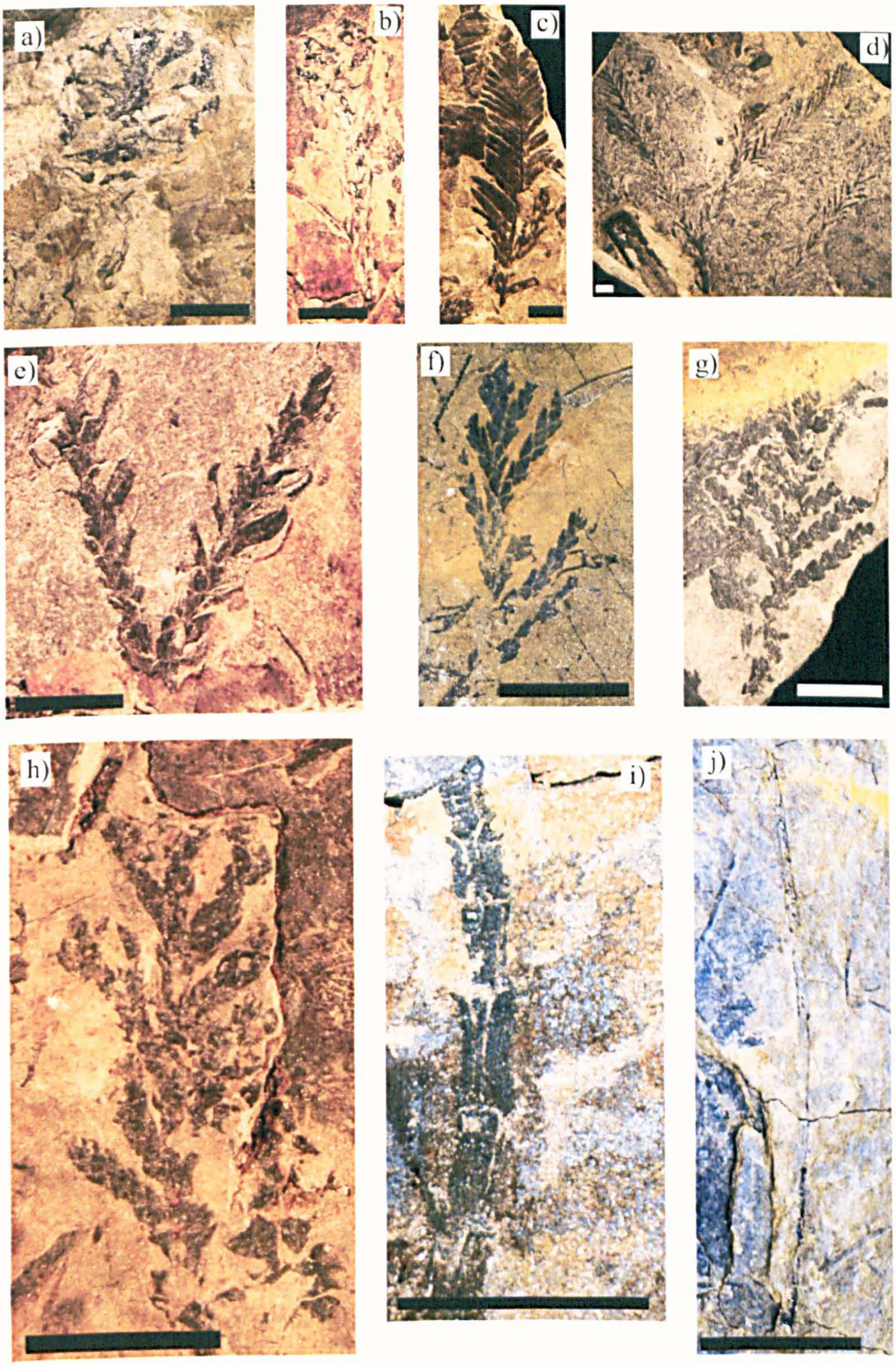

Figure 5.5.4. Representatives of conifer macrofossils from Allt Mor, Skye. a) ovulate cone of *Metasequoia occidentalis* (OC1), b) Ovulate cone of *Sequoia* sp. (OC2), c) CM1 *Metasequoia occidentalis* (NMS.G.2004.29.008-e), d) CM2 *Sequoia* sp. (NMS.G.2004.29.100-g), e) CM3 *Glyptostrobus dunoyeri* (NMS.G.2004.29.062-d), f) CM4 "*Chamaecyparis* cf." (AM.ACC.001-f), g) CM5 "*Thuja* cf.". (NMS.G.2004.29.003-c), h) CM6 *Mesocyapris* sp. (AM.L4.08.0004-c), i) CM7 "Calocedrus cf.". (NMS.G.2004.29.24-e), j) CM8 (AM.NA.078).

The macro-floral record of the Allt Mor assemblage shows that 23 plant taxa representing 15 angiosperm and eight conifer morphotypes were present on Skye during the Paleocene. Nine angiosperm families are represented by the macrofossils, although it may have been higher because four of the angiosperm morphotypes cannot be identified to family level (AM 12-15). Conifer family-level diversity was lower with only two families recorded. These plant taxa all appear to represent woody shrub or tree taxa, but no herbaceous or aquatic vegetation has been identified at any of the plant localities, although Morphotype 10, *Vitiphyllum*, may represent a liana if its affinities with the Vitaceae is correct.

5.2.1 Diversity and morphotype richness

Species richness is a measure of the total number of species within a given community or ecosystem and is the simplest measure of diversity (Magurran 1988). Species accumulation curves have been used in palaeobotanical studies to determine the effect that sampling effort has on capturing the species richness of plant assemblages (Wing and DiMichelle 1995). Enhanced sampling effort increases the probability that the majority of species will be sampled within a given assemblage until only the rarest taxa remain to be recorded. At this point increased sampling effort does not increase the number of species recorded. Species accumulation curves are produced from the cumulative number of species related to the sampling effort.

The production of a species accumulation curve for a fossil plant assemblage is vital in order to understand that the effort to collect from that assemblage was adequate to capture the species richness preserved within the assemblage. Determining that sampling effort was sufficient and most fossil species were collected has important implications for the interpretation of floral diversity and palaeoclimate.

To produce a species accumulation curve for the Allt Mor assemblage angiosperm leaves and conifer shoots were counted in each sample (rock slab). The Allt Mor collection includes 379 fossil-rich samples, which represents 2572 individual leaf or cone specimens. Each plant specimen was identified where possible to its corresponding conifer or angiosperm morphotype (each representing an individual 'bin') and its abundance on each slab was recorded. Specimens that could not be reliably identified were counted and put into bins specifically designated for groups of unidentifiable specimens (Table 5.3). The species accumulation curve for the Allt Mor assemblage was then produced using PAST statistical software (Hammer et al. 2001) (Figure 5.5).

Table 5.3. Unidentifiable macrofossil bin categories, description and morphotypes represented by these bins.

Macrofossil bin	Bin description	Probable morphotypes in this bin
unidentifiable conifers	conifer shoots whose identity cannot be determined	CM 1-8
unidentifiable Sequoioideae	Sequoioideae shoots that cannot reliably distinguished from CM 1 or 2	CM 1-2
unidentifiable Cupressoideae	Cupressoideae shoots that cannot be reliably distinguished from CM 4-7	CM 4-7
unidentifiable angiosperms	angiosperm leaf fragments too poorly preserved to determine the morphotype or primary venation	AM 1-15
unidentifiable pinnate angiosperms	angiosperm leaf fragments with pinnate primary venation that are too poorly preserved to identify to a pinnate morphotype	AM 3, 4, 5, 6, 7, 8, 10, 12, 13, 14, 15
unidentifiable palmate angiosperms	angiosperm leaf fragments with palmate leaf form that are too poorly preserved to identify to a palmate morphotype	AM 1, 2, 9, 11

CM = conifer morphotype, AM = angiosperm morphotype.

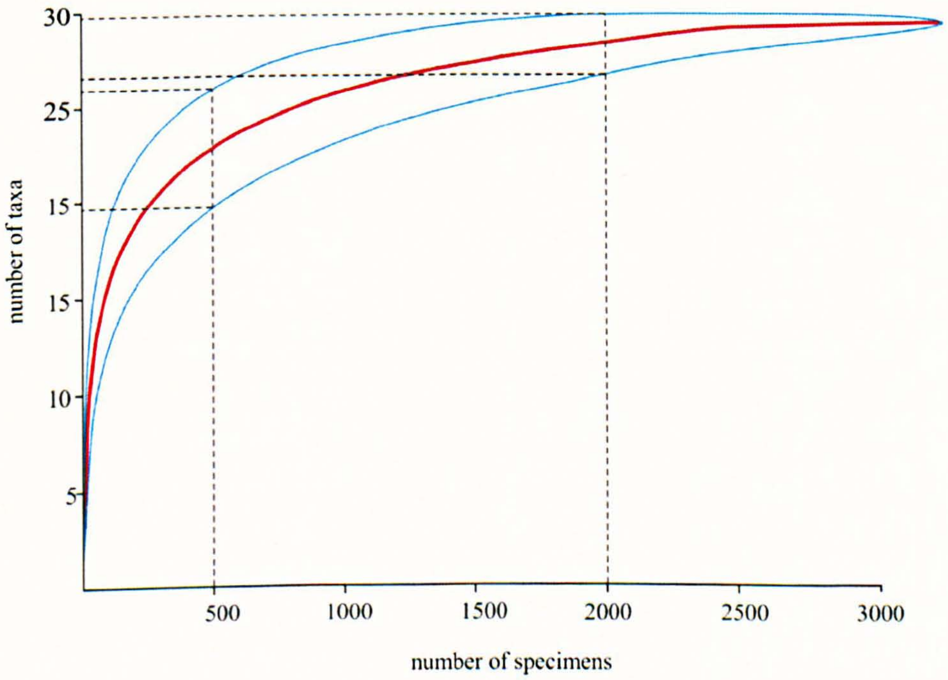

Figure 5.5. Species accumulation curve for the Allt Mor fossil plant assemblage. Blue lines represent 95% confidence intervals. Dashed lines refer to points where a high proportion or the maximum number of taxa within the assemble have been sampled.

The species accumulation curve indicates that between 15 to 25 of the taxa will be present within limited sampling effort of 500 specimens (Figure 5.5). To capture the remaining diversity significantly more sampling effort is required as the curve does not reach asymptote until ~2000 specimens are counted (Figure 5.5). The curve suggests that sampling effort in this study was sufficient to capture most of the floral diversity at Allt Mor. Future collections from this site require sampling of greater than 2000 specimens to discover the rarer taxa in this assemblage.

5.2.2 Relative abundance of floral elements

Determining the diversity and relative abundance of each fossil plant taxon can provide insight into the species and vegetation composition of fossil plant assemblages. For example the high relative abundance of specific taxa within a fossil assemblage can show that they are either locally or more regionally dominant members of the plant community (Hickey 1980, Burnham et al. 1992, Wing and DiMichelle 1995).

The relative abundance of each of the plant taxa from the Allt Mor assemblage has been determined by identifying and counting each fossil plant fragment (Table 5.4). In total 2572 individual conifer and angiosperm leaf fragments were counted and identified. Conifer shoots account for 55% of the specimens and angiosperms 45% of the specimens from the Allt Mor assemblage. The relatively higher abundance of conifer shoots may indicate ecological dominance but may be attributed to a variety of taphonomic processes, which are discussed in section 5.3.

Table 5.4. Relative abundance of the floral components of the Allt Mor assemblage.

morphotypes or unidentifiable bin types	number of specimens	% of specimens	abundance category
Conifers			
unidentifiable conifer	43	1.7	uncommon
unidentifiable Sequoioideae	253	9.8	common
unidentifiable Cupressoideae	131	5.1	common
CM1 *Metasequoia occidentalis*	251	9.8	common
CM2 *Sequoia* sp.	558	21.7	dominant
CM3 *Glyptostrobus dunoyeri*	99	3.9	uncommon
CM4 "*Chamaecyparis* cf."	23	0.9	rare
CM5 "*Thuja* cf."	36	1.4	uncommon
CM6 *Mesocyparis* sp.	2	0.1	rare
CM7 "*Calocedrus* cf."	1	>0.1	rare
CM8 Pinaceae-type	6	0.2	rare
Angiosperms			
unidentifiable angiosperm	230	8.7	common
unidentifiable pinnate angiosperm	452	17.5	dominant
unidentifiable palmate angiosperm	6	0.2	rare
AM1 *Platanites hebridicus*	104	4.0	uncommon
AM2 *Trochodendroides antiqua*	65	2.5	uncommon
AM3 *Corylites hebridicus*	197	7.7	common
AM4 "*Corylites* cf."	16	0.6	rare
AM5 *Fagopsiphyllum groenlandica*	3	0.1	rare
AM6 *Juglandiphyllites* sp.1	7	0.3	rare
AM7 *Juglandiphyllites* sp.2	1	>0.1	rare
AM8 "*Platycarya* cf."	47	1.8	uncommon
AM9 *Vitiphyllum sewardii*	8	0.3	rare
AM10 *Cornophyllum hebridicum*	4	0.2	rare
AM11 *Zizyphoides sp.*	16	0.6	rare
AM12 affinity unknown	1	>0.1	rare
AM13 affinity unknown	11	0.4	rare
AM14 affinity unknown	1	>0.1	rare
total number of specimens	2572		

CM = conifer morphotype, AM = angiosperm morphotype. Abundance categories defined by relative percentages of each taxon; rare, <1%; uncommon, 1-5%; common, 5%-10%; dominant >10%.

Specimen counts from the Allt Mor assemblage indicates that the majority of the specimens are attributed to a small number of morphotypes or bins (Table 5.4). The relative percentage of each morphotype/bin has been put into abundance categories (see Table 5.4) to express their importance in the flora. Two morphotypes/bins, CM2 (*Sequoia* sp.) and unidentifiable pinnate angiosperms are dominant components of the Allt Mor flora and account for ~39% of the specimens (Figure 5.6). Five common morphotypes/bins (unidentifiable Sequoideae, CM1 (*Metasequoia occidentalis*), unidentifiable angiosperms, AM3 (*Corylites hebridicus*) and unidentifiable Cupressoideae) are common components and collectively account for ~41% of the specimens (Figure 5.6). The remaining conifer and angiosperm morphotypes/bins are considered uncommon (~15%) or rare (~4%) components collection (Figure 5.6).

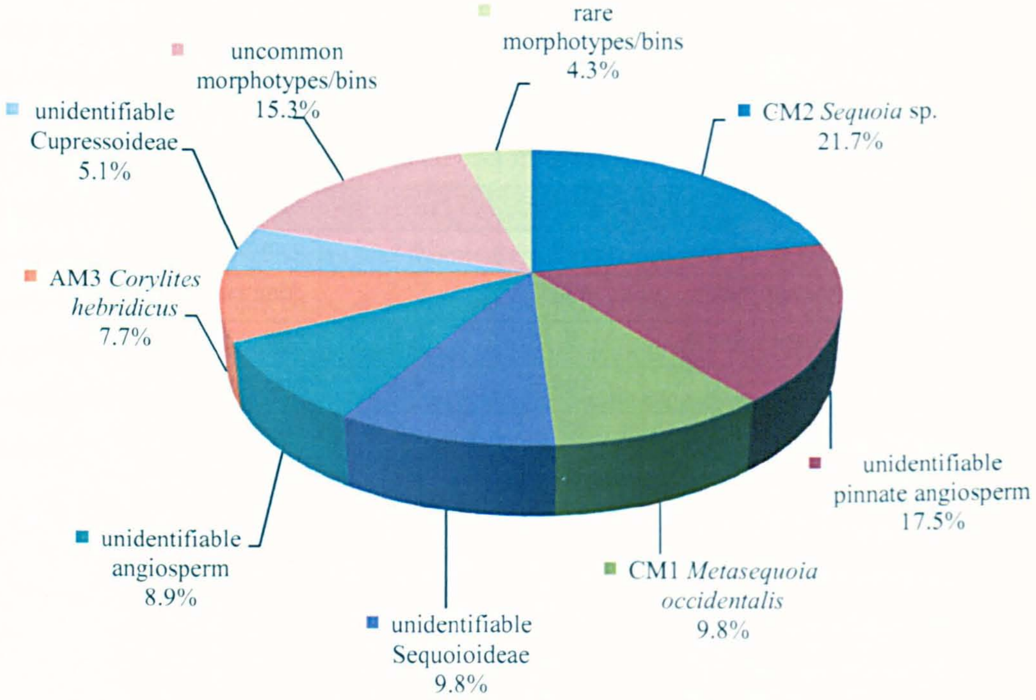

Figure 5.6. Relative abundance of conifer and angiosperm morphotypes and unidentifiable bins within the Allt Mor macrofossil assemblage. For details on the specific morphotypes or bins with these broader abundance categories see Table 5.4.

The dominant and common members of the assemblage are apparent from the counts (Table 5.4, Figure 5.6). These dominant and common taxa probably represent the local vegetation growing near to the depositional site at Allt Mor. This suggests the local vegetation was dominated by Sequoideae conifers such as *Metasequoia* (CM1) and *Sequoia* (CM2) with common occurrences of *Corylites* (AM3) and Cupressoideae conifers. The remaining uncommon or rare taxa may have originally been less abundant components of the vegetation, grew further away from the site of deposition or may have had limited preservation potential.

5.2.3 Floral habit and palaeoenvironment associations of the conifer and angiosperms morphotypes of Skye

Studies of modern vegetation and their associated environments have shown that the size of the plant, its habit and the community/environment that it grew in has a strong effect on the spatial patterns of leaf litter production and accumulation (Roth and Dilcher 1989, Spicer 1989, Burnham et al. 1992, Greenwood 1992). Determining these factors for fossil plants is difficult as specific taxa are typically represented by disarticulated organs, so reconstructing the whole plant is difficult or impossible. *In-situ* vegetation is not preserved in any of the Skye fossil assemblages so the standing structure of the source vegetation cannot be determined with confidence, but inferences from modern vegetation, the macrofossil and palynological assemblages from Skye and other Paleogene floras may provide some insight into the size of the plants, their habit and their palaeoenvironmental associations.

5.2.3.1 Growth habit of the Skye floras

The growth or floral habit of plant refers to its vegetative posture and height e.g. short stature shrub or canopy tree. Determining the growth habit of macrofossils from Skye will provide insight into the vegetation structure in this region during the mid Paleocene.

The relative height and possible growth habit of the Allt Mor conifers has been determined from comparisons with modern relatives and the *in-situ* remains of MacCulloch's Tree on Mull. The modern relatives of the Allt Mor conifers indicate that the fossil conifers were probably tall canopy trees (Table 5.5).

Table 5.5. The nearest living relatives (NLRs) of the Allt Mor conifers and their mature heights. Height of modern realtive from Eckenwalder (2009).

conifer morphotype	nearest living relative	mature height range (m)
CM1 *Metasequoia occidentalis*	*Metasequoia glyptostroboides*	35 to 60
CM2 *Sequoia* sp.	*Sequoia sempervirens*	up to 112
CM3 *Glyptostrobus dunoyeri*	*Glyptostrobus pensilis*	25
CM4 "*Chamaecyparis* cf'	*Chamaecyparis* spp.	30 to 65
CM5 "*Thuja* cf'.	*Thuja* spp.	10 to 50
CM6 *Mesocyparis* sp.	unknown	unknown
CM7 "*Calocedrus sp*"	*Calocedrus* spp.	23 to 46
CM8 Pinaceae-type	Pinaceae	2 to 100

MacCulloch's Tree (NG 580 468) is an *in-situ* conifer that was entombed by the lavas of the Staffa Formation on Mull (Figure 5.7). This tree provides the only evidence of *in-situ* arborescent vegetation from the BTVP. Although very little fossil wood remains, it is assumed that the trunk-shaped cavity formed around a standing tree. The tree was large, approximately 1 m wide and 12 m tall and is attributed to taxodiaceous conifers (Brown et al. 2009). The tree was growing in a swampy environment prior to the eruptions that preserved it (Emeleus and Bell 2005). The total height of MacCulloch's Tree cannot be determined as the upper portion of the trunk and canopy are not preserved. Its overall preserved proportions, however, indicate it was well within the height range of modern taxodiaceous conifers, such as *Metasequoia* and *Glyptostrobus* (Table 5.5).

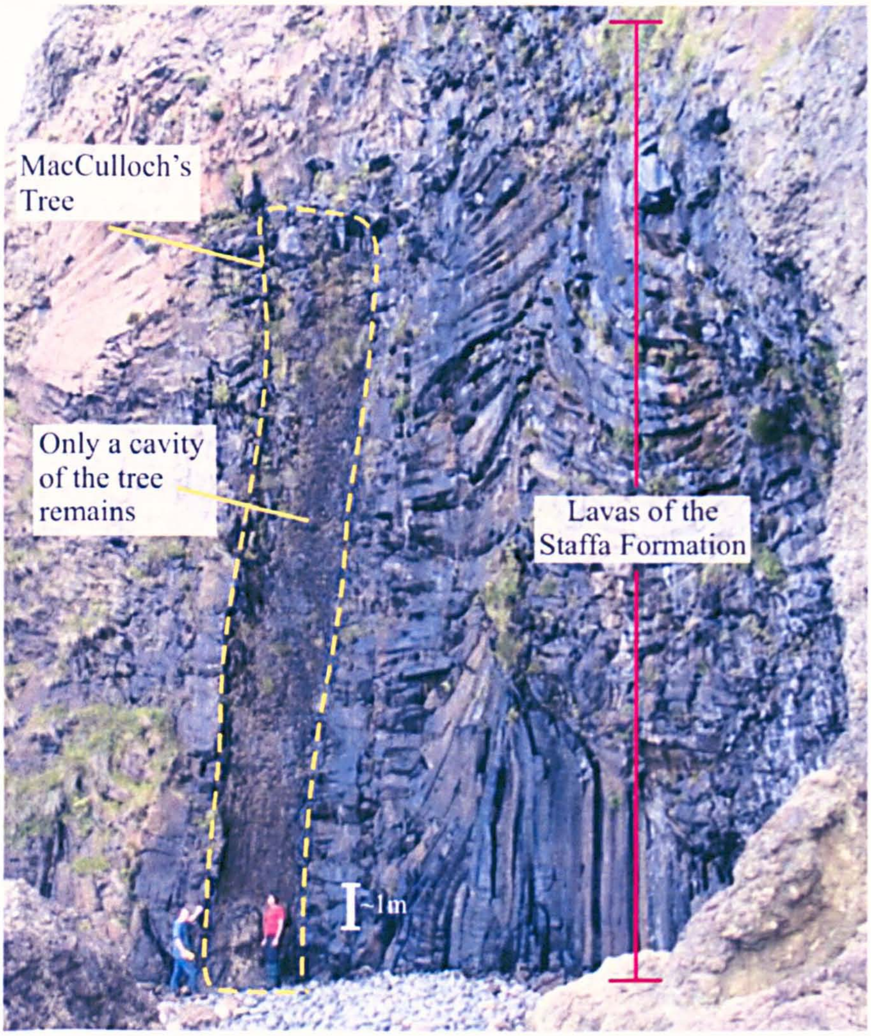

Figure 5.7. Photograph of MacCulloch's Tree of Mull (NG 580 468). The mould of the tree is preserved within the lavas of the Staffa Formation. Photograph taken by D. J. Brown http://www.davidjbrown.org.uk/DJB%20Scotland.htm. Annotated by Jon Poulter.

The large size of MacCulloch's Tree and the stature of modern relatives of the Sequoioideae and Cupressoideae fossils (Table 5.5) present at Allt Mor suggests that tall trees were a conspicuous element of the vegetation and they probably represented the climax canopy vegetation of Skye.

Determining the growth form of Paleogene angiosperms from their modern relatives is problematic as many of the families, including those found on Skye such as the Platanaceae, Cercidiphyllaceae, Betulaceae, Fagaceae and Juglandaceae, were diversifying rapidly during this interval (Upchurch and Wolfe 1987, Wing et al. 2005). A study by Upchurch and Wolfe (1987) showed that the physiognomy of modern woody dicotyledonous angiosperms reflects their growth habit. The morphology of the angiosperm leaf morphotypes from Skye may therefore provide some insight into their growth form.

Leaves with palmate venation, cordate bases, drip-tips, toothed margins, large lamina areas and short length:width ratios are characteristic of understory vegetation and liana habit. Vegetation growing in successional or disturbed habitats often have thin membranaceous leaves, with lobed and/or compound foliage. Climax vegetation in megathermal climates has thick coriaceous leaf textures and in meso-microthermal climates tends to have membranaceous leaves (Upchurch and Wolfe 1987). The development of different physiognomic suites is a response to the local growing conditions, for example, understory vegetation or lianas are subjected to limited light and high humidity under the canopy and have evolved particular leaf strategies to compensate for these conditions (Upchurch and Wolfe 1987).

The physiognomic characters previously mentioned were scored for each of the angiosperm leaf morphotypes from Allt Mor to determine their growth habit and how this might have affected their relative abundance in the vegetation The scored taxa were then analysed using cluster analysis to see if particular morphotypes formed specific groups that might represent past growth habits (Figure 5.8). The cluster analysis was generated using PAST statistical software (Hammer et al. 2001). Two algorithms were used to test the robustness of the clusters; unweighted paired grouping average and Ward's Method. The former algorithm clustering is based on the average distance between groups, whilst the latter, forms clusters that reduce within group variation.

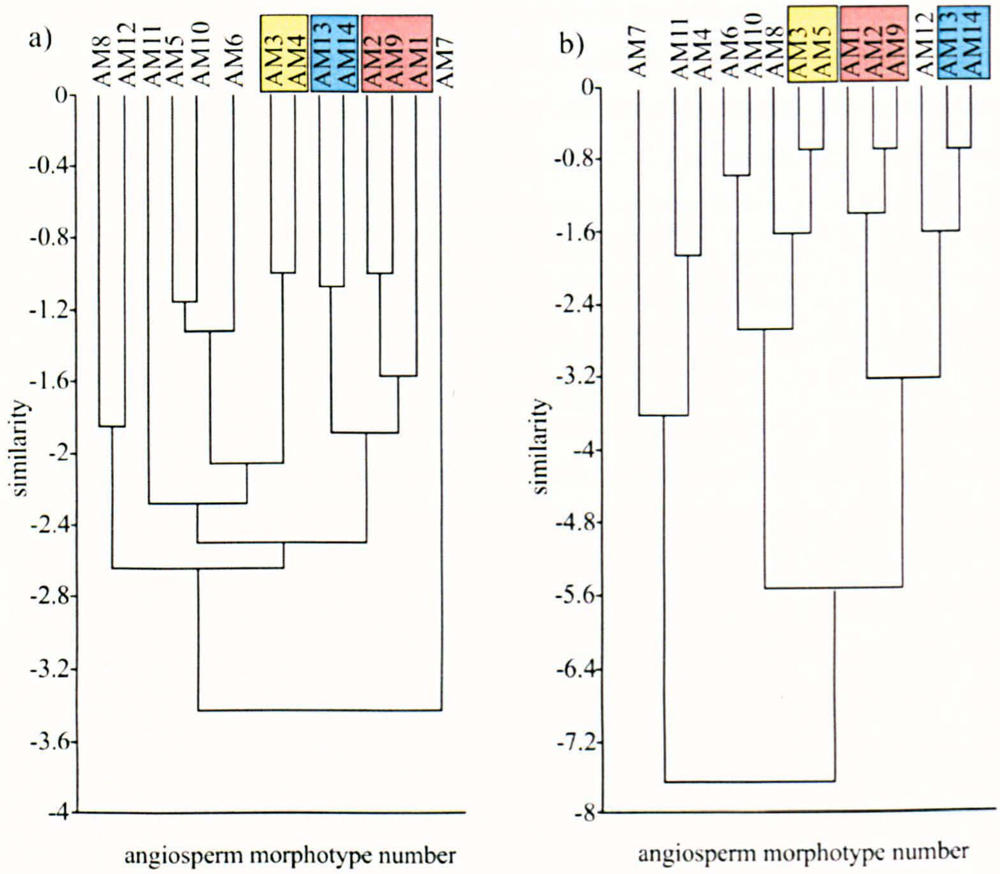

Figure 5.8. Dendrograms of leaf physiognomic data from angiosperm morphotypes of Allt Mor. a) Dendrogram using paired-grouping; b) dendrogram using Ward's Method. Coloured boxes represent consistent clusters using both algorithms.

Three stable groups were produced from the cluster analysis (Figure 5.8) and include the *Trochodendroides-Vitiphyllum-Platanites* (AM 2, 9, 1) group, a *Corylites hebridicus*-"*Corylites* cf" (AM 3, 4) group, and AM13-AM14 group. The remaining morphotype clusters were inconsistent, which indicates that their clustering is not reliable. The morphology of the *Trochodendroides-Vitiphyllum-Platanites* group is suggestive of understory and liana vegetation as the leaves are palmate, have cordate bases, toothed margins, large lamina areas and short length:width ratios. *Trochodendroides* and *Platanities* are likely understory shrubs or trees, while *Vitiphyllum*, with its association with the Vitaceae, was possibly a liana.

The *Corylites hebridicus*-"*Corylites* cf" group is clustered on their shared morphological attributes such as cordate base, drip-tips, toothed margin and large lamina areas. These taxa are also possible understory shrub or tree taxa which grew in the humid, dark conditions below the canopy. The AM13-AM14 group habit is less easily recognised as the morphology of both morphotypes is incomplete due the limited number of specimens and preservation.

Morphotype 8, *"Platycaraya cf"*, is the only angiosperm in the Allt Mor assemblage with compound leaf organisation, and includes one specimen (NMS.G.2004.29.66) with a rachis with three attached leaflets this indicates that it may have been a member of early successional, disturbed environments. *Platanites hebridicus* (AM1) may have also been adapted to these conditions as its leaf organisation and morphology suggest adaptations to these conditions. Well preserved specimens of the angiosperm from Mull show that the leaf organisation was trifoliate (one terminal leaflet and two lateral leaflets) and the terminal leaflets were near-lobate (Crane et al. 1988). These features indicate that this plant may have been well adapted to the understory and disturbed, successional environments.

The floral habits that can be determined from the fossil plant remains from Skye indicate that tall cupressaceous and taxodiaceous conifers may have created a closed or shaded canopy (Table 5.6). The shaded, humid conditions of the understory contained a variety of angiosperm shrubs, trees and possibly a liana (Table 5.6). Disturbed conditions and open succesional environments are indicated by the two angiosperm taxa *Platanites hebridicus* (AM1) and *"Platycaraya cf"* (AM8) (Table 5.6).

Table 5.6. Suggested growth habit types present on Skye and their associated morphotypes.

Habit	Morphotype
Canopy forming vegtaion	OC1/CM1 *Metasequoia occidentalis* OC2/CM2 *Sequoia* sp. OC3/CM4 "*Chamaecyparis* cf." CM5 "*Thuja* cf." CM8
Understorey	AM1 *Platanites hebridicus* AM2 *Trochodendroides antiqua* AM3 *Corylites hebridicus* AM4 "*Corylites* cf."
Liana	AM9 *Vitiphyllum sewardii*
Successional vegetation	AM1 *Platanites hebridicus* AM8 "*Platycarya* cf."

5.2.3.1 Palaeoenvironmental associations of the macrofossil floras of Skye

Combined evidence from the nearest living relatives of the Skye macrofossils, their relative abundance and palynological associations indicates that the plants that produced the macrofossils may have grown in a variety of palaeoenvironments and communities (Table 5.7). Three broad palaeoenvironmental facies are suggested: riparian, swamp and upland (Table 5.7). Riparian vegetation refers to plants growing in and around fluvial environments. Swamp conditions represent riparian environments with elevated water-table and waterlogged soils. Upland palaeoenvironments refer to extra-basinal conditions i.e. environments distal to the floodplain such as valley sides and tops and areas of elevated topography outside of the palaeovalleys.

The leaf deposits of Skye were produced by fluvial deposition (Williamson and Bell 1994) and thus fossil leaves in these deposits are therefore likely to be dominated by local riparian vegetation. Sequoioideae (CM 1-2) and Cupressoideae conifers (CM 4-7) are among the most abundant components of the Allt Mor floral assemblage (Table 5.4), which indicates that these conifers grew in or close to riparian environments (Table 5.7). Pollen attributed to these conifers is widespread and abundant across Skye (Jolley 1997) suggesting they were dominant taxa in riparian ecosystems. Modern representatives of these conifers are tolerant of flood-related disturbance, but may have developed in areas of the floodplain where flooding was less intense or infrequent, such as the distal margins of the floodplains (Eckenwalder 2009, Naiman et al. 2010).

The most abundant angiosperms of the Allt Mor assemblages (*Corylites* (AM3), *Platanites* (AM1) and *Trochodendroides* (AM2)) probably thrived in riparian environments (Table 5.7). Pollen associated with these taxa has been found in sediments associated with floodplain settings (Jolley 1997). This is consistent with other Paleogene riparian communities in the Northern Hemisphere, which often contain high abundances of these taxa (Crane and Stokey 1985, McIver and Basinger 1994, Gemmil and Johnson 1997, Pigg and DeVoire 2009).

Table 5.7. Suggested palaeoenvironmental association of plant macrofossils from Skye, based on environmental preferences of their modern relatives, macrofossil and palynological evidence.

morphotype	nearest living relative	modern environment	palaeoenvironment	evidence
Conifers				
CM1 *Metasequoia occidentalis*	*Metasequoia glyptostroboides*	riparian/upland	swamp/riparian/upland	1, 2, 3
CM2 *Sequoia* sp.	*Sequoia sempervirens*	riparian/upland	riparian/upland	1, 2, 3
CM3 *Glyptostrobus dunoyeri*	*Glyptostrobus pensilis*	riparian/swamp	swamp/riparian	1, 3
CM4 "*Chamaecyparis* cf"	Cupressoideae	riparian/upland	riparian/upland	1, 3
CM5 "*Thuja* cf"	Cupressoideae	riparian/upland	riparian/upland	1, 3
CM6 *Mesocyparis* sp.	Cupressoideae	riparian/upland	riparian/upland	1, 3
CM7 "Calocedrus cf"	Cupressoideae	riparian/upland	riparian/upland	1, 3
CM8 Pinaceae-type	*Pinaceae*	upland	upland	1, 2, 3
Angiosperms				
AM1 *Platanites hebridicus*	Platanaceae	riparian/upland	riparian	1, 2, 3
AM2 *Trochodendroides antiqua*	Cercidiphyllaceae	riparian	riparian	1, 2, 3
AM3 *Corylites hebridicus*	Betulaceae	riparian/upland	riparian	1, 2, 3
AM4 "*Corylites cf*"	?Ulmaceae	riparian/upland	riparian	3
AM5 *Fagiosiphyllum groenlandica*	Fagaceae	riparian/upland	riparian/upland?	3
AM6 *Juglandiphyllites* sp.1	Juglandaceae	riparian/upland	swamp/riparian?	1, 2
AM7 *Juglandiphyllites* sp.2	Juglandaceae	riparian/upland	swamp/riparian?	1, 2
AM8 "*Platycarya cf*"	Juglandaceae/*Platycarya*	riparian/upland	riparian	1, 2, 3
AM9 *Vitiphyllum sewardii*	Vitaceae	riparian/upland	understory	1
AM10 *Cornophyllum hebridicum*	Cornaceae	riparian/upland	riparian	1, 2
AM11 *Zizyphoides sp.*	Trochodendraceae	riparian/upland	riparian	1, 2

CM = conifer morphotype, AM = angiosperm morphotype. Evidence: 1) modern relatives, 2) macrofossils of Skye, 3) Palynological evidence from Skye (Jolley 1997).

Floral inhabitants of swamp conditions are primarily indicated by pollen assemblages, which are dominated by taxodiaceous and juglandaceous pollen (Jolley 1997). Modern forms of *Metasequoia* and *Glyptostrobus* are well adapted to swamp conditions, which suggest they were capable of growing in these conditions in the past (Eckenwalder 2009). This association is confirmed from the Paleogene record of these plants as swamp deposits are often dominated by one or both of these plant taxa e.g. in the Paleogene forests of the Canadian Arctic (Greenwood and Basinger 1994, Pigg and DeVoire 2009). Three angiosperm morphotypes (AM 6-8) have been recognised from Allt Mor and may represent the juglandacous component of these swamps.

Palynological evidence from the Skye Lava Group indicates that conifers attributed to the Cupressaceae and Pinaceae were widespread and were abundant components of the plant communities on Skye during the Paleocene (Jolley 1997). As suggested previously, several members of the Cupressaceae may have been components of riparian communities but their abundance in the pollen record and the tolerances of their modern relatives may indicate that they grew in upland environments as well (Table 5.7). Jolley (1997) suggested from his interpretations of the pollen record that members of the Pinaceae dominated the upland areas of Skye. This interpretation is partially indicated by the macrofossil record of the Pinaceae, which is composed of six poorly preserved needles, possibly indicating that they were growing away from the riparian environments due to their rarity in the macrofossil record.

5.3 Taphonomy

Fossil plant assemblages can provide information on the original diversity and structure of the vegetation, but the fidelity to which they reflect the original vegetation is dependent on how they were accumulated and how they are interpreted (Roth and Dilcher 1978, Spicer 1981, Scheihing and Pfefferkorn 1984, Ferguson 1985, Burnham 1989, Spicer 1989, Greenwood 1992, Behrensmeyer et al. 1992, Burnham et al. 1992, Gastaldo et al. 1995). The fossil plant assemblages of Skye provide a record of the vegetation that grew in this region during the Paleocene, but to what degree do these assemblages accurately portray the standing vegetation? For source vegetation to become fossilised it has to be subjected to a variety of processes (Figure 5.9). These processes can greatly affect the composition of the fossil plant assemblages and can lead to a biased or skewed perspective of the vegetation. Careful analysis and interpretation of these processes are required to interpret the original vegetation accurately as discussed in the following sections.

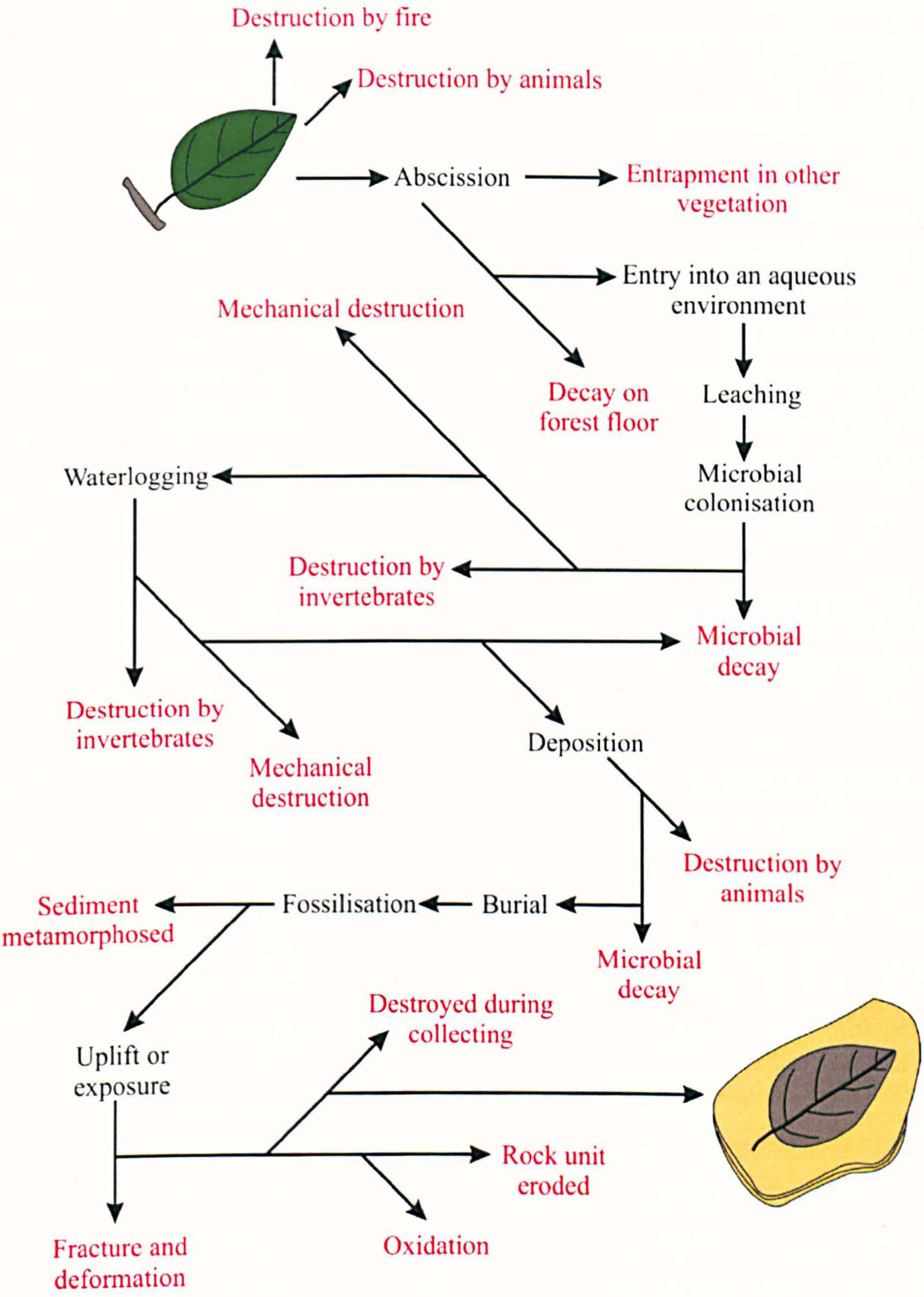

Figure 5.9. Fossilisation pathway of leaf, red text denotes destructive processes of fossil plant material. Figure provided by Robert Spicer.

5.3.1 Pre-depositional factors

5.3.1.1 Abscission: deciduous or evergreen leaf habit

Abscission, the shedding of leaves and other plant organs, is the first stage of fossilisation; abscission however, is not uniform across all vegetation. Herbaceous angiosperms and ferns do not typically abscise their leaves and so have little chance of being preserved (Spicer 1981, Ferguson 1985). Arborescent angiosperms and conifers do abscise their foliage but at different rates and times of year depending on whether they are deciduous or evergreen (Ferguson 1985, Burnham 1989, Burnham et al. 1992). Abscission therefore represents the first bias in a fossil plant assemblage as some taxa have a greater chance of entering the depositional setting assemblage than others. Deciduous leaves are shed en-mass and in large numbers and so have a greater chance of being incorporated in an assemblage (Spicer 1981, Ferguson 1985). Deciduous leaves are, however, less resistant to decay compared to evergreen leaves (Ferguson 1985) and therefore may have a reduced chance of surviving transport and preservation.

To investigate this potential bias, the conifer and angiosperm leaf morphotypes from Skye and their modern relatives were examined to determine if they were deciduous or evergreen, and their relative abundance in the assemblage assessed (Tables 5.8, 5.9). Three morphological characters were considered: coriaceous leaf texture (thick leaf texture), the presence of a drip-tip, and the presence of an entire margin, as these may be characteristic of evergreen habit (Upchurch and Wolfe 1987). The leaf habit of modern conifer relatives in Table 5.8 was taken from Echenwalder (2009) and for the angiosperms the database of Watson and Dallwitz (1992 onwards) was used.

Table 5.8. Conifer morphotypes of the Allt Mor assemblage, their nearest living relatives and their leaf habit.

morphotype	nearest living relative	deciduous	evergreen
conifers			
CM1 *Metasequoia occidentalis*	*Metasequoia glyptostroboides*	X	
CM2 *Sequoia* sp.	*Sequoia sempervirens*		X
CM3 *Glyptostrobus dunoyeri*	*Glyptostrobus pensilis*	X	
CM4 "*Chamaecyparis* cf."	*Chamaecyparis spp?*		X
CM5 "*Thuja* cf."	*Thuja spp*?		X
CM6 *Mesocyparis* sp.	Cupressoideae		X
CM7 "*Calocedrus cf.*"	Cupressoideae		X
CM8 Pinaceae-type	Pinaceae		X

Comparison with the modern relatives of the conifers from Allt Mor suggests that two of the eight conifer taxa were deciduous, *Metasequoia* and *Glyptostrobus*, and the remaining six morphotypes could have been evergreen (Table 5.8). The deciduous conifer taxa should theoretically be more abundant in the assemblage as they shed their short shoots synchronously, which should increase input of shoot material into the assemblage. Data from the Allt Mor assemblage (Table 5.4), however, shows that evergreen conifers account for ~29% of the plant fragments, while deciduous conifers account for only ~14%. The majority of the evergreen conifer fragments (21%) are attributed to *Sequoia* sp. (conifer morphotype 2), while the remaining evergreen taxa collectively account for ~7%. This indicates that either evergreen conifer remains were preferentially preserved or that evergreen conifers were the dominant tree types.

It is important to note that overall abundance of deciduous and evergreen conifers is incomplete because unidentifiable Sequoioideae were not included. This unidentifiable group could contain both deciduous *Metasequoia* and evergreen *Sequoia*, which would shift the ratio of relative abundance of deciduous or evergreen types.

The angiosperm morphotypes of Allt Mor, based on their morphology and nearest living relatives, appear to dominated by deciduous types, their abundance within the assemblage may be due synchronous leaf fall at the end of the growing season.

5.3.1.2 Other factors that influence pre-depositional biases in leaf assemblages

Studies that compare the forest structure with litter accumulation have shown that the relative abundance of tree taxa within a forest is reliably reflected in the leaf litter accumulations (Burnham 1989, Burnham et al. 1992, Greenwood 1992). Leaf litter accumulations on forest floors have not undergone transport or sorting that other fossil leaf assemblages have. Studies that have determined the effect that transport and sorting have on leaves in a variety of sedimentary environments have shown that dominant or common taxa in the source vegetation still preserve their relative abundance (Spicer 1989, Greenwood 1992, Gastaldo et al. 1995). The relative abundance of particular taxa within an assemblage can also be influenced by the height of the plants that produced them and their proximity to the site of deposition (Ferguson 1985, Burnham et al. 1992).

The Allt Mor assemblage is dominated by macrofossil remains of tall conifers and riparian plants, which suggests that this assemblage is preserving a biased, local record of the vegetation structure. The presence swamp vegetation such as members of the Juglandaceae (AM 6-8) and *Glyptostrobus* (CM3), and upland trees attributed to the Pinaceae (CM8) and the Cupressaceae (CM6-7) show that representatives from a variety of palaeoenvironments were preserved in the assemblage at Allt Mor (Table 5.7). The presence of plants that were non-riparian indicates that vegetation from more a regional area has been preserved at Allt Mor. Regional representatives are highly diluted by the local vegetation signal as these plants taxa (AM 6-8, CM6-8) are either uncommon or rare components of the assemblage (Table 5.4).

5.3.2 Depositional factors that influenced leaf preservation and accumulation

5.3.2.1 Overview of the types of plant macrofossil assemblages

Each depositional environments is characterised by particular processes and depositional patterns, which in turn can produce different plant assemblages (Roth and Dilcher 1978, Burnham 1989, Spicer 1989, Behrensmeyer et al. 1992). The energy and degree of transport that plant debris is subjected to will affect its potential for preservation and the composition of the deposit (Spicer 1989). Three broad assemblage types have been recognised: autochthonous, parautochthonous and allochthonous, each representing varying degrees of transport of plant material and associated depositional environments.

Autochthonous assemblages contain fossil plant material that was produced *in-situ* and has undergone no transport; these assemblages therefore provide a reliable record of the standing local vegetation (Behrensmeyer et al. 1992). This assemblage type is characteristic of swamp, marsh or mire conditions where plant material is accumulated and preserved *in-situ* (Spicer 1989).

Parautochthonous assemblages represent plant fossils that have either been produced *in-situ* or have been transported a short distance but are still characteristic of the local riparian vegetation. Depositional environments such as abandoned channels or small lakes produce parautochthonous assemblages (Gastaldo et al. 1995).

Allochthonous assemblages include accumulations of plant debris that have been transported from their original source and deposited in a more distal location. Allochthonous assemblages can therefore provide a more regional perspective of the vegetation as plant material has been sourced from a wider catchment area. This assemblage type is associated with a variety of sedimentary environments or deposits such as crevasse-splay, overbank or channel lag deposits (Spicer 1989).

The depositional environment and the preservation of the plant fossils on Skye evaluated to determine how the plant material accumulated at Allt Mor, and to which assemblage type it belongs.

5.3.2.2 Depositional setting of Allt Mor

The Allt Mor plant assemblage is preserved within the Allt Mor Member of the Minginish Conglomerate Formation, which was interpreted by Williamson and Bell (1994) as deposition within a broad, fault-controlled valley that ran from the southeast to the northwest and drained by a braided river system. The conglomerates deposited by this fluvial system show regolith production to the south near to the Rum central volcano. Associated with the channel deposits are overbank sand and siltstones indicative of floodplain environments. These sediments often grade into localised silt and coal deposits, which represent swamp development. Debris flow deposits indicate instability at the margins of the valley sides. It is probable that tributaries flowed from the valley sides and may have transported plant material from the upland area. This depositional setting could therefore have allowed the growth of a variety of plant communities that were influenced by disturbance, water level and topography. Fossil leaves could have been sourced from a variety of plant communities within the broader catchment area or may represent one of these environments.

The sediments of the Allt Mor plant assemblage represent a natural depression on the underlying lava surface which formed a ponded environment. This pond was progressively filled with overbank and higher energy flood event sedimentation. The leaf material is most abundant and best preserved in the fine grained, laminated siltstones but plant debris, including leaves, occur in the coarser silt and sandstone units. This site appears to have become vegetated at one stage because a thin palaeosol (~5 cm) with abundant rootlets in the sediments below suggest that the pond deposit was colonised by vegetation. This phase of stability appears to have been short-lived as the silt and sandstones above the palaeosol suggest flooding smothered the vegetated surface. These sediments are typical of overbank deposition and possible swamp development observed elsewhere in the Minginish Conglomerate Formation (Williamson and Bell 1994).

The sediments of the Allt Mor plant assemblage appear to have be derived from low intensity overbank deposition and higher energy flooding events (see Chapter 2, Figure 2.10). These sediments could therefore have preserved plant material from both the local area and more regional sources (Figure 5.10). The fine grained, laminated silts represent overbank deposition and low energy levels. Leaf material from these deposits probably represents both local vegetation growing at the pond margin and riparian plants of the floodplain (Figure 5.10). The coarser siltstone and sandstone beds lack lamination and appear to have been deposited by higher energy flooding events and could have incorporated local and riparian elements, as well as plant debris transported and accumulated from the larger catchment area of the valley (Figure 5.10).

The Allt Mor plant beds show similar facies patterns as abandoned channels, as they are composed of fine to medium grained clastic fluvial sediments, which in many cases become vegetated during the later stages of their development (Gastaldo et al. 1995). Plant assemblages recovered from these environments are composed of autochthonous vegetation such as macrophytes (aquatic plants) and parautochthonous elements such as marginal vegetation and riparian elements (Gastaldo et al. 1995). Abandoned channels are typically characterised by fining upwards sequences related to waning energy levels and reduced inflow into the channel and eventual stabilisation and plant colonisation (Gastaldo et al. 1995). This pattern is partially observed in Allt Mor assemblage but coarser units occur throughout sequence. These coarser deposits indicate that the river channels were in close proximity to the pond and coarser silts and sands from the channel's bed-load were periodically deposited into the assemblage. The deposition of the channel sediments would have increased the influx of allochthonous elements into the assemblage.

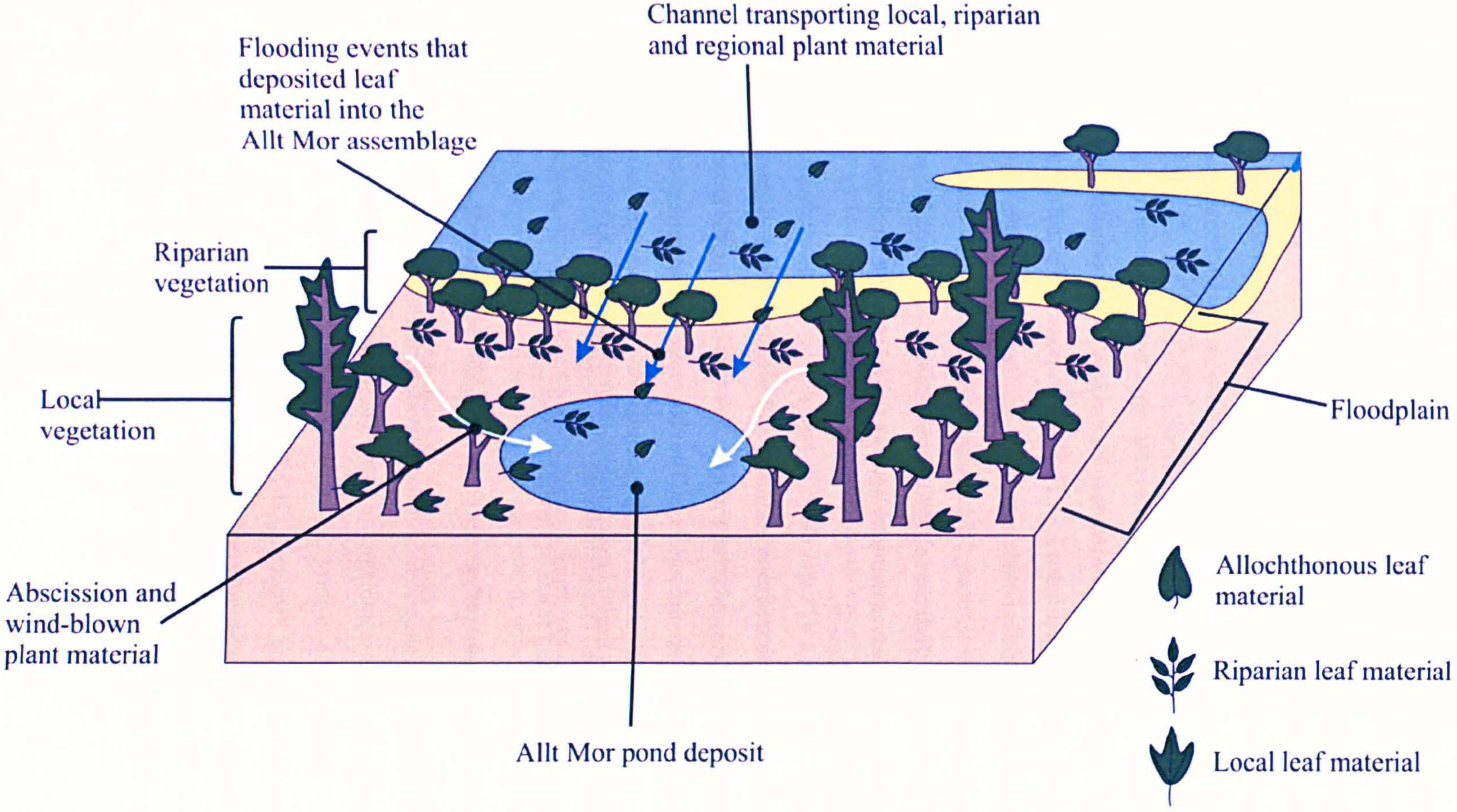

Figure 5.10. Conceptual diagram of the Allt Mor leaf assemblage palaeoenvironment and vegetation.

5.3.2.3 Size and fragmentation of the leaves

To assess the relative inputs of allochthonous, autochthonous and parautochthonous elements within the Allt Mor assemblage the size and degree of fragmentation of the angiosperm leaves was assessed. Several studies have shown that leaves that have undergone transport become progressively more fragmented and sorted (Roth and Dilcher 1978, Spicer 1981, Ferguson 1985). Larger leaves are less well represented if transport has taken place as they may become entangled or entrapped more easily, and tend to sink faster (Ferguson 1985). If the assemblage at Allt Mor is dominated by small highly fragmented leaves it would indicate that transport of the leaf material had taken place.

A sub-sample of 720 angiosperm leaves from the Allt Mor assemblage were scored based on their degree of fragmentation and their lamina areas, see Chapter 3 (sections, 3.5.1 and 3.5.6). The distribution of leaf fragments indicates that there is bias towards smaller leaf fragments within the Allt Mor assemblage (Figure 3.5). The high proportion of small fragments (91%) and fragment (8%) is indicative of degradation and damage. The fragmentation may have arisen through immersion and microbial decay, but appears to be limited as the leaves show little skeletonisation (loss of mesophyll tissue), which is associated with this process (Ferguson 1985). Fragmentation of the leaves therefore appears to be a result of mechanical damage of the lamina through transport processes.

The distribution of angiosperm leaf size within the Allt Mor assemblage is skewed to smaller leaf areas (figure 3.10). This suggests that transport has winnowed out the larger leaves, leaving smaller fragmented leaves in greater numbers. The size range of the angiosperm morphotypes and estimated original areas of some of the fragmented leaves indicates the leaves, prior to transport, were of a larger size. This indicates that the observed size of the angiosperm fragments appears to be a direct result of fluvial transport.

5.3.3 Summary of depositional influences on the Allt Mor leaf assemblage

Investigation of multiple taphonomic factors has provided insight into the controls on the deposition of the fossil plant assemblages on Skye. These assemblages represent localised accumulations of plant debris and show that mixed conifer and angiosperm forests developed in fluvial environments during the Paleocene. The Allt Mor assemblage is dominated by Sequoioideae conifers such as *Sequoia* and *Metasequoia* with common occurrences of Cupressoideae conifers and the broad-leaved angiosperm *Corylites*. These taxa probably represent the local riparian vegetation growing close to the pond deposit and surrounding floodplain.

The abundance of conifer taxa, particularly those with evergreen habit, is related to their tall stature and resistance to decomposition and transport. These factors have favoured their preservation and abundance within the assemblage. Accelerated decomposition of deciduous elements does not appear to have been a significant preservational bias as deciduous angiosperms are highly abundant in the assemblage.

The most abundant angiosperm taxa (*Corylites*, *Platanites* and *Trochodendroides*) may have been preferentially preserved because they were originally abundant members of the community. The physiognomy of *Corylites*, *Platanites* and *Trochodendroides* indicates they were understory trees or shrubs and so should have limited preservation potential. The relative abundance of these understory angiosperms suggests they grew close to the site of deposition at Allt Mor or areas of active transport and sedimentation such as channel margins or floodplains.

Pond deposits, such as those at Allt Mor, typically contain plant debris that has autochthonous and parautochthonous origin (Gastaldo et al. 1995). The pond deposit at Allt Mor lacks any plants in growth position such as macrophytes (aquatic plants). Parautochthonous elements are present as local vegetation and floodplain taxa, including Sequoioideae conifers and angiosperms such as *Platanites*, *Corylites*, *Trochodendroides* and "*Platycarya* cf.".

The fragmentation and small lamina size of the angiosperm leaves indicates mechanical damage, which is attributed to fluvial transport and indicates that a high proportion of the angiosperm leaf material has been sourced from a broader catchment area. This may indicate that the Allt Mor assemblage contains both local, parautochthonous elements as well as regional, allochthonous elements.

The suggestion that the assemblage provides regional floral information is supported by the high abundance of rare taxa, which account for 83% of the richness but only 4% of the specimens. These rare taxa may represent more distal regional vegetation, which through transport has been winnowed to a few individual leaves by the time of deposition at Allt Mor. The Allt Mor assemblage therefore appears to represent both local and more regional aspects of the flora.

5.4 Palynological evidence of Paleocene vegetation on Skye

5.4.1 Paleocene palynological record of Skye

Palynological evidence from Skye provides important information that can help determine the more regional floral diversity and vegetation composition. The macrofossil remains from Skye described in this study can then be compared to the palynomorph assemblages to help determine how they fit within the regional context. Palynology can also provide evidence on the overall diversity and relative abundance of the floras within the larger catchment area, which may not be apparent from the more locally derived leaf assemblages.

Palynomorph assemblages have been collected from multiple sites across Skye and indicate a moderately diverse flora grew in this region during the Paleocene (Jolley 1997). Sedimentary sequences within the west-central and northern Skye lava fields were sampled for their palynomorph content (Figure 5.11). All sites were characterised by low to moderately diverse palynomorph assemblages with low abundances of individual grains and poor preservation (Jolley 1997).

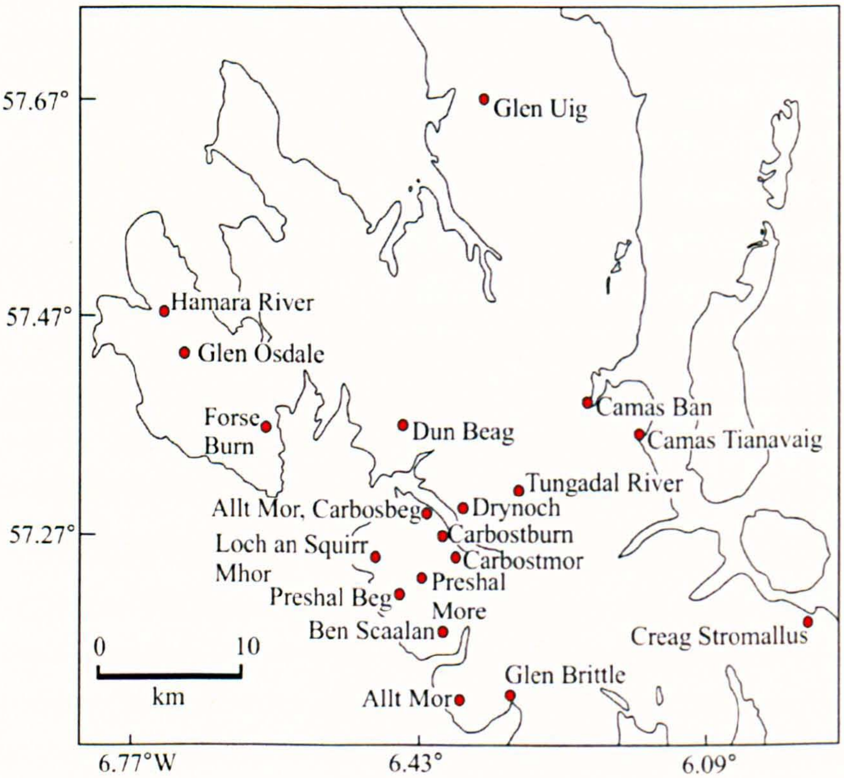

Figure 5.11. Map showing palynological sample sites from Paleocene interbasaltic sediments of Skye. Redrawn from Jolley (1997).

A review of Jolley's (1997) data for this study indicates that there are several inconsistencies with the data. It is difficult or impossible to determine accurate palynomorph counts from the figures, and on several occasions the values for one sample contain greater than 100% palynomorph specimens. Comparisons of the palynomorph assemblages between sites indicates that there is little correlation (Figures 5.12, 5.13, Table 5.10), this is perhaps due to limited recovery of suitable numbers of palynomorphs coupled with poor preservation. The apparent lack of correlation between sites suggests that the palynomorphs from the Paleocene of Skye are not suitable for stratigraphic correlation or dating. Despite these limitations, the work by Jolley (1997) can still provide some insight into the overall diversity of the Skye floras, as well as possible palaeoenvironment associations. The following review represents a summary of the palynology at several localities and the interpretations made by Jolley (1997). Relative abundances of each taxa were converted to categories 'rare', 'uncommon', 'common' and 'dominant' for each locality and presented in Figures 5.12 and 5.13.

The palynomorph assemblages on Skye were interpreted by Jolley (1997) to indicate five distinct palaeosurfaces, which represented periods of volcanic quiescence when sedimentary environments and vegetation developed on the lava surfaces. Each palaeosurface is represented by a variety of palynomorph assemblages that equate to specific community types and palaeoenvironments (Jolley 1997), (Table 5.9).

Table 5.9. Palaeosurfaces of the Skye Lava Group, their representative palynofloral assemblages and associated palaeoenvironments, based on the study by Jolley (1997).

palaeosurface	palynofloral assemblage(s)	palaeoenvironment(s)
E1	Juglandaceae and Taxodiaceae swamp flora	swamp
E2	upland taxodiaceous forest streamside angiosperm communities montane Pinaceae dominated forest	upland forest riparian montane forest
E3	Juglandaceae dominated swamp Juglandaceae/fern swamp angiosperm/fern floodplain community montane Pinaceae dominated forest	isolated swamp swamp riparian montane forest
E4	upland taxodiaceous forest streamside angiosperm communities montane Pinaceae dominated forest	upland forest riparian montane forest
E5	Juglandaceae dominated swamp angiosperm/fern floodplain community upland taxodiaceous forest, montane Pinaceae dominated forest	isolated swamp riparian upland forest montane forest

Table 5.10. Palynomorph taxa from interbasaltic sediments of Skye showing their affinities, relative abundance and localities in which they occur.

palynomorph taxon	family affinity	AM(E2)	TR (E3)	AMC (E3)	DB (E4)	HR (E5)	GO (E5)
Fungi							
Multicellaesporites spp.	fungi	common	P				
Pesavis tagluensis	fungi				P		
Bryophyta							
Stereisporites (S.) steroides	Bryophyta		common		P		uncommon
Filicopsida							
Deltoidospora adriennis	Cyathaceae				uncommon		
Laevigatosporites haardtii	?Blechnaceae, ?Thelypteridaceae		dominant				uncommon
Leiotriletes adriennis	?Schizaeaceae	rare			uncommon		uncommon
Gymnospermae							
Piceapollis spp.	Pinaceae	uncommon	rare		rare		rare
Pityosporites haplox	Pinaceae				common		
Pityosporites diplox	Pinaceae				uncommon		
Pityosporites spp.	Pinaceae		rare	rare	uncommon		uncommon
Inaperturopollenites dubius	Taxaceae/Cupressaceae				common		
Inaperturopollenites distichiforme	Cupressaceae (syn. Taxodiaceae)			rare			
Inaperturopollenites hiatus	Cupressaceae (syn. Taxodiaceae)	dominant		dominant	rare	dominant	uncommon
Sequoiapollenites polyformosus	Cupressaceae (syn. Taxodiaceae)			uncommon			
Sciadopityspollenites serratus	Sciadopityaceae		rare				
Bisaccate pollen undif.	Coniferopsida		common				
Monocolpopollenites tranquilus	Ginkgoaceae	rare	rare	rare			rare

Locality codes; AM, Allt Mor (E2); TR, Tungadal River (E3); AMC (E3), Allt Mor, Carbostbeg; DB, Dun Beag (E4); HM, Hamara River (E5); GO, Glen Osdale (E5). Abundance categories; rare, <5%; Uncommon, 5-15%; Common, 15-30; dominant, >30%).

palynomorph taxon	family affinity	AM (E2)	TR (E3)	AMC (E3)	DB (E4)	HR (E5)	GO (E5)
Angiospermae							
Alnipollenites verus	Betulaceae			rare			rare
Cupuliferiopollenites cingulum fusus	Fagaceae			rare		uncommon	
Cupuliferiopollenites cingulum oviformis	Fagaceae			rare			
Liquidambarpollenites stigmosus	Hamamelidaceae				rare		
Momipites anellus	Juglandaceae			uncommon			
Momipites tenuipolus	Juglandaceae		rare	uncommon			dominant
Momipites cf. *tenuipolus*	Juglandaceae			P			
Momipites spp.	Juglandaceae			rare			
Platycaryapollenites platycaryoides	Juglandaceae			rare			rare
Plicatopollis plicata	Juglandaceae						rare
Nyssapollenites krushi analepticus	Nyssaceae			rare			
Retitricolpites retiformis	Platanaceae	rare	P	rare	rare		rare
Retitricolpites anguloluminosus	Platanaceae		P				
Triatriopollenites subtriangulus	Myricaceae			rare			
Tricolpites hians	Platanaceae/Cercidiphyllaceae?	rare	uncommon	rare		common	rare
Erdtmanipollis pachysandroides	?Buxaceae			P			
unknown affinity							
Radialisporites radiatus				P			
Pediastrum bifidites							P
Total palynomorphs counted		121	598	1335	532	11	523

Locality codes; AM, Allt Mor (E2); TR, Tungadal River (E3); AMC (E3), Allt Mor, Carbostbeg; DB, Dun Beag (E4); HM, Hamara River (E5); GO, Glen Osdale (E5). Abundance categories; rare, <5%; Uncommon, 5-15%; Common, 15-30; dominant, >30%).

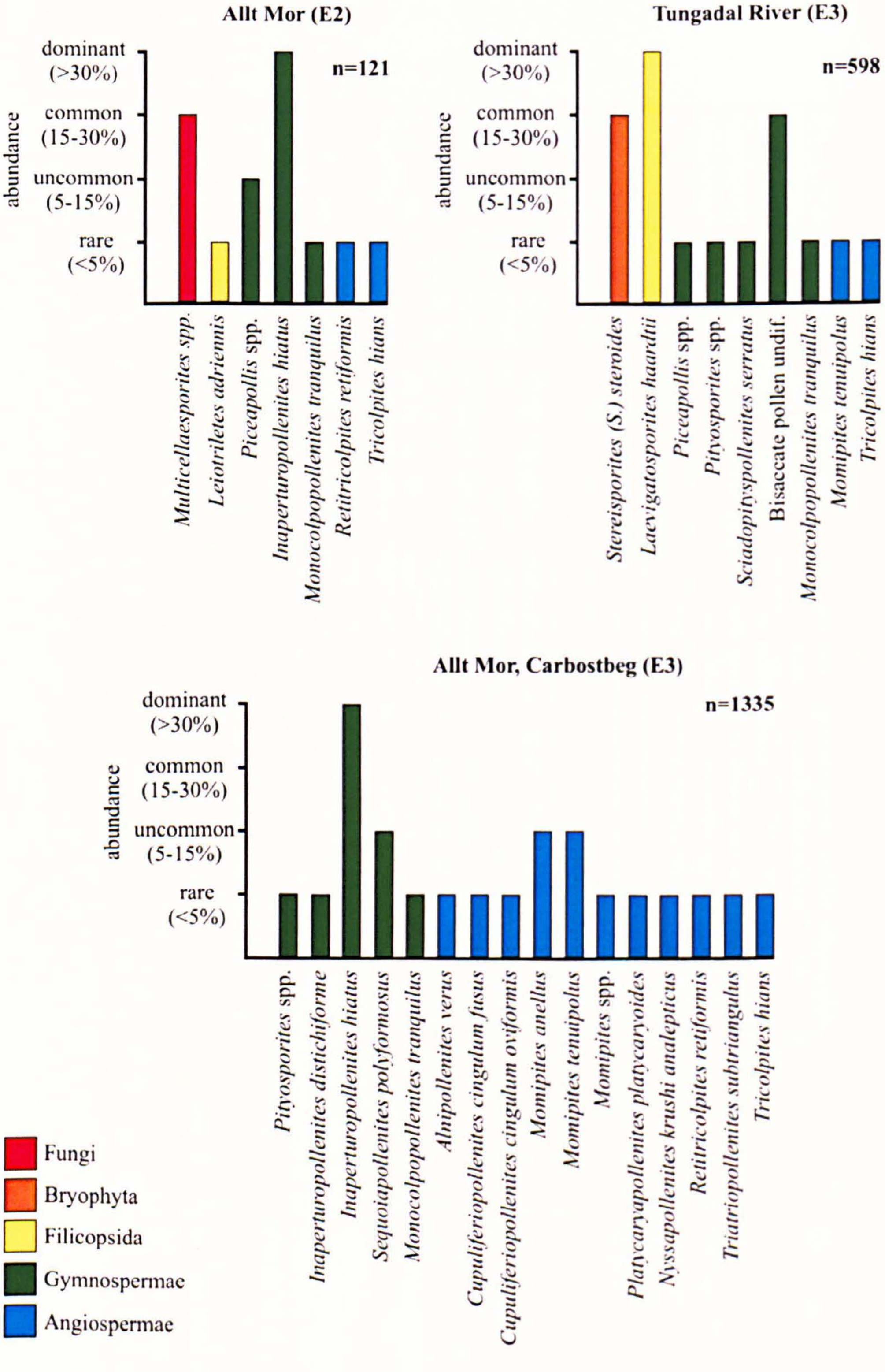

Figure 5.12. Relative abundance of palynomorph taxa from samples collected from inter-basaltic sediments from Allt Mor (E2), Tungadal River (E3) and Allt Mor, Carbostbeg (E3). n= number of palynomoprhs counted for site. Data from Jolley (1997) and replotted by Jon Poulter.

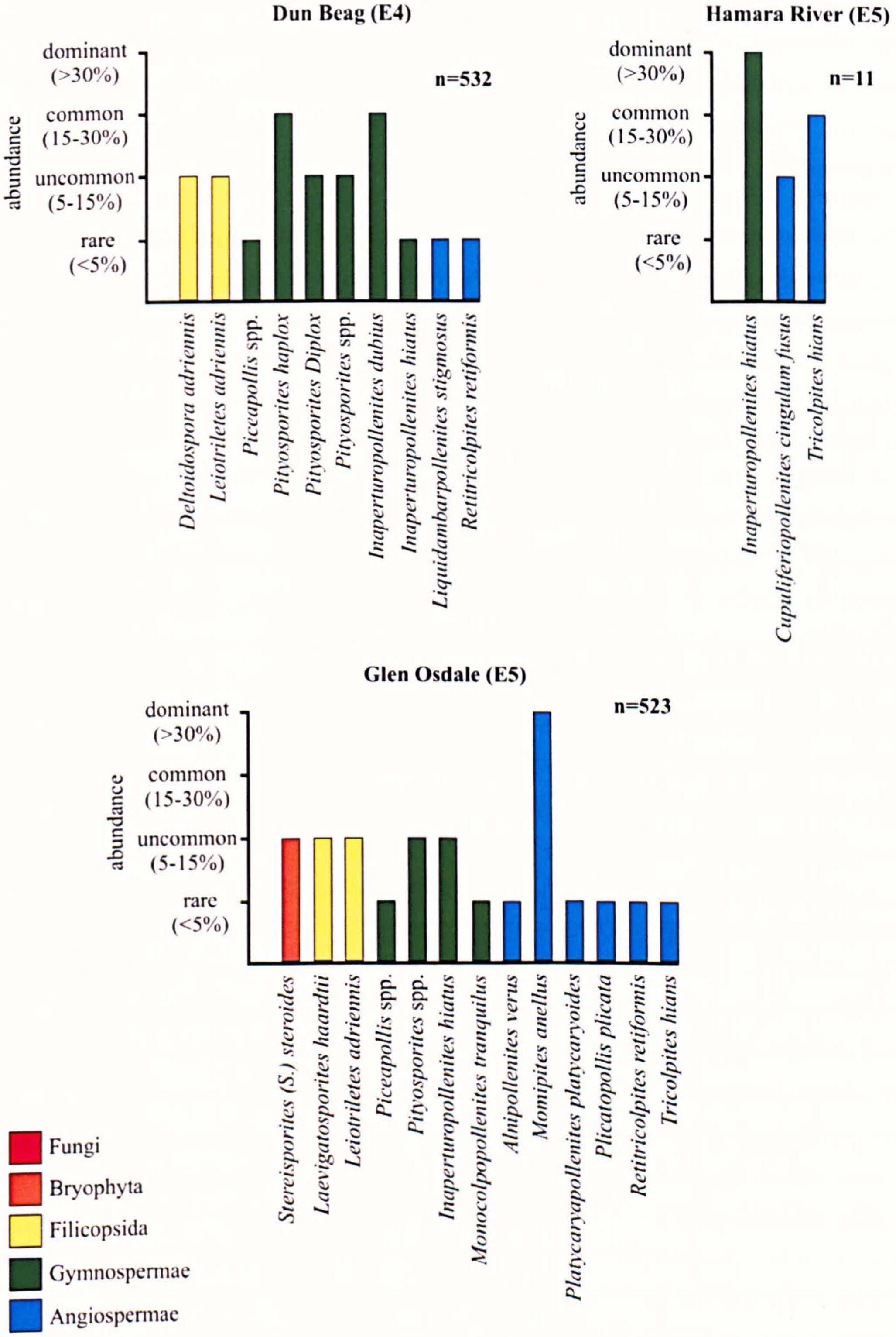

Figure 5.13. Relative abundance of palynomorph taxa from samples collected from interbasaltic sediments from Dun Beag (E4), Hamara River (E5) and Glen Osdale (E5). n = number of palynomoprhs counted for each site. Data from Jolley (1997) and replotted by Jon Poulter.

The oldest palaeosurface, called E1, was derived from the Palagonite Tuffs in north and eastern Skye, which represent the earliest phases of volcanic activity of the Skye Lava Group (Anderson and Dunham 1966). Samples were collected from Camas Ban, Glen Uig and Camas Tianavaig, but the latter was the only site to yield palynomorphs (Jolley 1997) (Figure 5.11). The sedimentary sequence consisted of thin red boles with tuffs, shales and coals.

Jolley (1997) suggested that this assemblage represents a lowland swamp flora dominated by *Taxodium* and juglandaceous angiosperms. This interpretation is partially confirmed by the sedimentology of the Palagonite Tuffs which were considered by Anderson and Dunham (1966) to represent deposition in a lowland basin, possibly in saline waters. The high proportion of subangular, equidimentional black wood within the samples was suggested by Jolley (1997) to represent both high degrees of oxidation and possible wildfires.

The second palaeosurface identified by Jolley (1997), E2, is of most direct relevance for this study as the sedimentary deposits are from the Minginish Conglomerate Formation, which includes the Allt Geodh' a' Ghamhna and Allt Mor plant assemblages. As outlined in Chapter 2 the sedimentary environments of Minginish Conglomerate Formation were interpreted as a braided river system with overbank and localised swamp development. Although Jolley (1997) states that samples were collected from several sites in this sedimentary formation, only one sample is presented in the study and is from the Allt Mor Member. The sample from Allt Mor is limited, with a total of 121 palynomorphs, and represents a low diversity assemblage of seven palynomorph species (Figure 5.12, Table 5.10) (Jolley 1997). The palynoflora is dominated by taxodiaceous conifer pollen, Pinaceae pollen and rare angiosperm pollen that comprises less than 5% of the assemblage.

The palynomorph assemblage of surface E2 was interpreted by Jolley (1997) as representing an upland taxodiaceous conifer forest, with a cyathacean fern understory with streamside angiosperm communities dominated by taxa associated with the Platanaceae. The low diversity of the palynomorph assemblage at Allt Mor and the interpretation of the flora by Jolley (1997) contrasts with the interpretation of the macrofossils described in this study, and will be discussed in section 5.4.2.2.

The third palaeosurface interpreted by Jolley (1997), surface E3, is represented by sedimentary sequences in west-central Skye between the Glen Caladale and Fiskavaig Lava Groups. The sediments of this quiescent interval were not recognised in the Williamson and Bell (1994) study and have no formal nomenclatural status. Jolley (1997) describes the sediments that outcrop at Carbost Burn, Tungadal River and Allt Mor, Carbostbeg (Figure 5.11) as purple and reddened shales with minor coaly laminae. The palynomorph assemblages recovered from the Allt Mor, Carbostbeg locality have yielded the richest and most diverse samples from the Skye

Lava Group. Twenty two palynomorph taxa were recognised and are associated with fungi (1 species), bryophytes (1 species), ferns (2 species), conifers (4 species), *Ginkgo* (1 species) and angiosperms (13 species) (Figure 5.12, Table 5.10).

The samples from Allt Mor, Carbostbeg are dominated by taxodiaceous conifer and juglandaceous pollen. Two other taxa that occur commonly in the samples include fern spores of *Laevigatosporites haardti* and platanaceous/cercidiphyllaceous angiosperm pollen of *Tricolpites hians*. The palynomorph assemblage shows some evolutionary changes with *Sequoiapollenites polyformosus* and *Cupuliferoipollenites cingulum* becoming increasingly abundant higher in the sequence.

The assemblage at the Tungadal River section is similar to that of Allt Mor, Carbostbeg with dominant *Inaperturopollenites hiatus* and *Momipites*, although the latter is more abundant at this locality. Fern spores become increasingly abundant higher in the sequence with *Laevigatosporites haardti* accounting for up to ~68% and *Leiotriletes adriennis* ~20% of the uppermost sample.

The palynofloras of the E3 surface have been interpreted by Jolley as representing a variety of palaeoenvironments and source vegetation types. The abundant and diverse assemblage at the Allt Mor, Carbostbeg locality represents an isolated swamp community dominated by members of the Juglandaceae. The increasing abundance of *Sequoia* and angiosperm pollen higher in the sequence is suggested by Jolley (1997) to reflect increasing drying of the swamp and the development of mixed angiosperm/conifer community. The Tungadal River section is interpreted as a Juglandaceae-dominated swamp community similar that of Allt Mor, Carbost Beg but with a richer fern component, which developed in close proximity to a fluvial system. The abundance of palynomorphs attributed to ferns and angiosperms indicates a better drained angiosperm/fern floodplain community. The presence of conifer pollen attributed to the Pinaceae is suggested by Jolley (1997) to have been sourced from higher elevated montane conifer forest.

Palaeosurface E4 corresponds to the Eynort Mudstone Formation in west-central Skye. The extensive boles and red brown mudstones deposits occur above the Fiskavaig Lava Group and are overlain by the Gleann Oraid and Loch Dubh lava groups. The sedimentary units sampled by Jolley (1997) were taken from Loch an Sguirr Mhoir and Dun Beag (Figure 5.11). These sites yielded poor palynomorph recovery, but several samples contained high frequencies of *Inaperturopollenites dubius*, *Liquidambarpollenites stigmosus*, *Deltoidspora adriennis* and *Pitysporites diplox* and *P. haplox*.

Jolley's (1997) interpretation of the depositional environments of surface E4 suggests an environment influenced by weathering and runoff. The lateritic composition of the sediments was suggested to represent both unvegetated weathered flow tops and areas with greater stability and pedogenesis. In the lowland areas small ephemeral lakes developed which were supplied with the products of the weathered lava surface. The palynofloras of E4 were interpreted by Jolley (1997) as representing humid pine and taxodiaceous conifer forests in the upland areas with stream side angiosperm communities.

The yougest palaeosurface recognised by Jolley (1997), surface E5, corresponds to the Preshal Beg Conglomerate Formation of west-central Skye (see Chapter 2, section 2.4), which overlies the Gleann Oraid Lava Group and is overlain by the Talisker Lava Group. These sediments were correlated by palynological evidence with sites in northern Skye at Hamara River and Glen Osdale (Figure 5.11), the latter of which has provided macrofossils described in this study. Samples were collected from the finer grained facies of the Preshal Beg Conglomerate Formation at Preshal More (Figure 5.13), but were reported by Jolley (1997) to be limited (Table 5.11). The palynomorphs that were present were interpreted as representing an upland taxodiaceous conifer forest with angiosperm-dominated streamside and swamp communities.

The sediments from the Hamara River locality yielded low numbers of palynomorphs (Figure 5.13) and so could not provide a reliable interpretation of the flora. Glen Osdale however, provided much richer samples representing a moderately diverse assemblage (Figure 5.13, Table 5.11). The most abundant components of the flora include *Momipites tenuipolus*, *Inaperturopollenites hiatus*, *Pitysporites* spp, *Laevigatosporites haardti* and *Stereisporites* (*Stereisporites*) *stereioides* (Jolley 1997). Jolley (1997) interpreted the palynomorph assemblages at Glen Osdale as representing a variety of plant communities including montane conifer forest, taxodiaceous dominated upland forests, juglandaceous-rich swamp communities, angiosperm floodplain forests dominant in platanaceous types and low-nutrient iron-rich soil bogs.

5.4.2 Comparison of the leaf and cones macrofossil with the palynomorphs of Skye

5.4.2.1 Plant families represented by the macrofossil and microfossils

The palynomorphs recovered from the interbasaltic sequences of Skye have provided an important record of the taxonomic composition of the Paleocene vegetation of this region. Thirty four palynomorph taxa were identified by Jolley (1997) which represent one bryophyte, three ferns, eleven gymnosperms, sixteen angiosperm species, two fungal types and one chlorophycean alga (Table 5.11). The affinities of these palynomorphs were presented in part in Jolley (1997), although were not comprehensive and the remaining affinities were determined from Jolley et al. (2009), and are presented in tables 5.11 and 5.12. Where possible, the macrofossil morphotypes of the conifers and angiosperms recovered from the plant beds of Skye are compared to the taxonomically-related palynomorphs.

The botanical affinities of the micro and macrofossils are similar for many of the conifers and angiosperm taxa, which suggests that the macro record of these plants is well represented in the palynological record. The palynological evidence, however, indicates that a wider range of taxonomic plant groups were present, including bryophytes, ferns, conifers, *Ginkgo* and angiosperms whereas only conifers and angiosperms have been recognised from the macrofossil assemblages on Skye in this study. This indicates that several plant types were either absent from the environments close to these depositional sites or have limited preservational potential. The palynological record is therefore an important record of these missing taxa.

Conifer pollen indicates that there were four families present, representing the Cupressaceae, Taxaceae, Pinaceae and Sciadopityaceae. Only two of these families (the Cupressaceae and Pinaceae) are represented by leaf and cone macrofossils from Skye. Four pollen species are attributed to the Cupressaceae (Table 5.11), while there are seven macrofossil taxa. Jolley (1997) attributes the Cupressaceae pollen to taxodiaceous types such as *Metasequoia*, *Sequoia* and *Taxodium*, but makes no mention of Cupressoideae conifers, which are both diverse and abundant in the macrofossil record. The limited diversity of Cupressaceae in the pollen record may be masked by the limited taxonomic variability and convergence prevalent in this family (Kunzmann et al. 2009), and one pollen taxon may represent multiple macrofossil species or genera.

Pinaceae macrofossils are rare and poorly preserved and appear to represent a single genus or species, which is in contrast to the pollen record which has four species representing this family. The pollen record of the Pinaceae indicates these conifers were relatively diverse, widespread and abundant whereas the rarity of these conifers in the macro-record is related to their limited preservation potential as they probably grew in more distal, possibly upland settings.

Fern spores are a common component of the interbasaltic sequences on Skye (Jolley 1997), but no fern leaves have been preserved. The absence of their macrofossils is related to their limited preservation potential as they do not abscise their leaves and require strong currents to remove the leaves. The fluvial deposits at Allt Geodh' a' Ghamhna and Glen Osdale are indicative of high energy flooding and may have had the potential to preserve fern fronds, but fern remains have not been observed, probably due to the limited sample size of these collections, but may indicate that the fern spore producers grew away from the sites of active sedimentation.

Pollen of *Monocolpopollenites tranquilus* indicates that *Ginkgo* was present on Skye during the Paleocene. Macrofossils of this gymnosperm have not been observed in this study but were reported from the Palagonite Tuffs of Northern Skye by Anderson and Dunham (1966), which confirms their presence.

Table 5.11. Filicopsida and Gymnosperm families in the Skye floras as represented by macrofossils and palynomorphs.

taxonomic group/family	macrofossil morphotype	palynomorph
Filicopsida		
Cyathaceae	none	*Deltoidospora adriennis*
?Blechnaceae, ?Thelypteridaceae	none	*Laevigatosporites haardtii*
?Schizaeaceae	none	*Leiotriletes adriennis*
Gymnosperms		
Cupressaceae	CM1 *Metasequoia occidientalis* CM2 *Sequoia* sp. CM3 *Glyptostrobus dunoyeri* CM4 "*Chamaecyparis* cf." CM5 "*Thuja* cf." CM6 *Mesocyparis* sp. CM7 "*Calocedrus* cf."	*Inaperturopollenites dubius* *Inaperturopollenites distichiforme* *Inaperturopollenites hiatus* *Sequoiapollenites polyformosus*
Pinaceae	CM8	*Piceapollis* spp. *Pityosporites haplox* *Pityosporites diplox* *Pityosporites* spp.
Sciadopityaceae	none	*Sciadopityspollenites serratus*
Ginkgoaceae	none	*Monocolpopollenites tranquilus*

CM= conifer morphotype

Angiosperm pollen and macrofossils are the most diverse element of the Skye floras with 16 pollen species and 14 leaf morphotypes identified. The family link of the pollen and leaves is possible to determine for many of the taxa (Table 5.12). The families Platanaceae, Cercidiphyllaceae, Betulaceae, Fagaceae and Juglandaceae are represented by both pollen and leaf macrofossils (Table 5.12).

Pollen associated with the Juglandaceae are the most diverse and often abundant component of the palynoflora (Jolley 1997) and is partially reflected in the macrofossil record as three morphotypes are attributed to this family. Pollen of *Platycaryapollenites platycaryoides* is attributed to *"Platycarya* cf.", as both share affinities with the genus *Platycarya*. The other Juglandaceae morphotypes cannot be reliably associated with particular pollen taxa.

The remaining eight angiosperm leaf types cannot be linked with pollen taxa as their own affinity is unknown or pollen attributed to their family has not been recovered from Skye. One pollen species *Triatriopollenites subtriangulus* is widespread across Skye and is associated with the Myricaceae (Jolley 1997). Leaves with Myricaceae affinity have not been found in any of the leaf assemblages on Skye, which suggests that the pollen producer had limited preservation potential or grew in more stable environments away from sites of deposition.

Table 5.12. Angiosperm families in the Skye flora as represented by macrofossils and palynomorphs.

family	macrofossil morphotype	palynomorph
Platanaceae	AM1 *Platanites hebridicus*	*Retitricolpites retiformis* *Retitricolpites anguloluminosus* *Tricolpites hians?*
Cercidiphyllaceae	AM2 *Trochodendroides antiqua*	*Tricolpites hians?*
Betulaceae	AM3 *Corylites hebridicus* AM4 "*Corylites* cf."	*Alnipollenites verus*
Fagaceae	AM5 *Fagopsiphyllum groenlandica*	*Cupuliferiopollenites cingulum fusus* *Cupuliferiopollenites cingulum oviformis*
Juglandaceae	AM6 *Juglandiphyllites* sp. 1 AM7 *Juglandiphyllites* sp. 2 AM8 "*Platycarya* cf."	*Momipites anellus* *Momipites tenuipolus* *Momipites* cf. *tenuipolus* *Momipites* spp. *Platycaryapollenites platycaryoides* *Plicatopollis plicata*
Vitaceae	AM9 *Vitiphyllum sewardii*	none
Cornaceae	AM10 *Cornophyllum hebridicum*	none
Trochodendraceae	AM11 *Zizyphoides flabella*	none
Myricaceae	none	*Triatriopollenites subtriangulus*
Altingiaceae	none	*Liquidambarpollenites stigmosus*
?Buxaceae	none	*Erdtmanipollis pachysandroides*

AM = angiosperm morphotype

5.4.2.2 Comparison of macrofossil and palynomorph record of Allt Mor

The palynomorph assemblage from Allt Mor presented in Jolley (1997) is poorly preserved and low in abundance and richness. As mentioned in section 5.4.1, Jolley (1997) interpreted the vegetation of this deposit as an upland taxodicaeous (sub families Sequoioideae and Taxodioideae) conifer forest with streamside angiosperm communities, with higher stands of pines. This interpretation is partially reflected in the leaf record of Allt Mor, as Sequoioideae foliage attributed to *Metasequoia* and *Sequoia* are the most abundant components of the assemblage (Figure 5.14). The streamside angiosperm community is also well represented in the leaf record by *Platanites* and *Trochodendroides*, which are among the most abundant angiosperm components of the flora (Figure 5.14). Pinaceae pollen present in the Allt Mor assemblage is matched by the rare occurrence of Pinaceae needles (Figure 5.14).

The leaf assemblage however, is considerably more diverse and potentially more representative of the community (Figure 5.14). Indeed, the leaf record contains representatives from many of the assemblage types interpreted by Jolley (1997). Three morphotypes (Morphotypes 6-8) are attributed to the Juglandaceae, whose pollen is absent from the assemblage but abundant in the swamp communities interpreted by Jolley (1997) elsewhere on Skye. *Corylites hebridicus* (AM3), a betulaceous representative in the Allt Mor assemblage, is the most common angiosperm taxon in the leaf record but pollen attributable to this family is absent. Indeed, only two species of angiosperm pollen have been recovered from Allt Mor and account for less than five percent of the palynomorphs counted. This is in contrast to the 14 angiosperm leaf morphotypes that have been identified from this site.

This trend is also observed in the conifers where eight leaf morphotypes have been recognised and only three pollen species have been recovered. Although the macrofossils are more diverse, there are palynomorph taxa present that are not present in the macrofossil record. Fern spores and *Ginkgo* pollen are present in low abundances but so far no leaf remains attributable to these plants have been identified.

The palynological record of the Skye Lava Group and its interpretation by Jolley (1997) suggests that the topography of the lava field and pre-Paleogene landscape led to the development of heterogenous vegetation cover. The current macro-floral record from the Skye Lava Group is based on a more limited sample area and therefore cannot provide a detailed view of the regional vegetation. The composition of the floras that have been studied, however, suggest that the interpretations of Jolley (1997) may be more related to preservational or interpretation errors rather than true ecological signals. This appears to be the case for the Allt Mor assemblage as 2572 leaf fragments have been identified, while only 121 individual palynomorphs have been collected from this site.

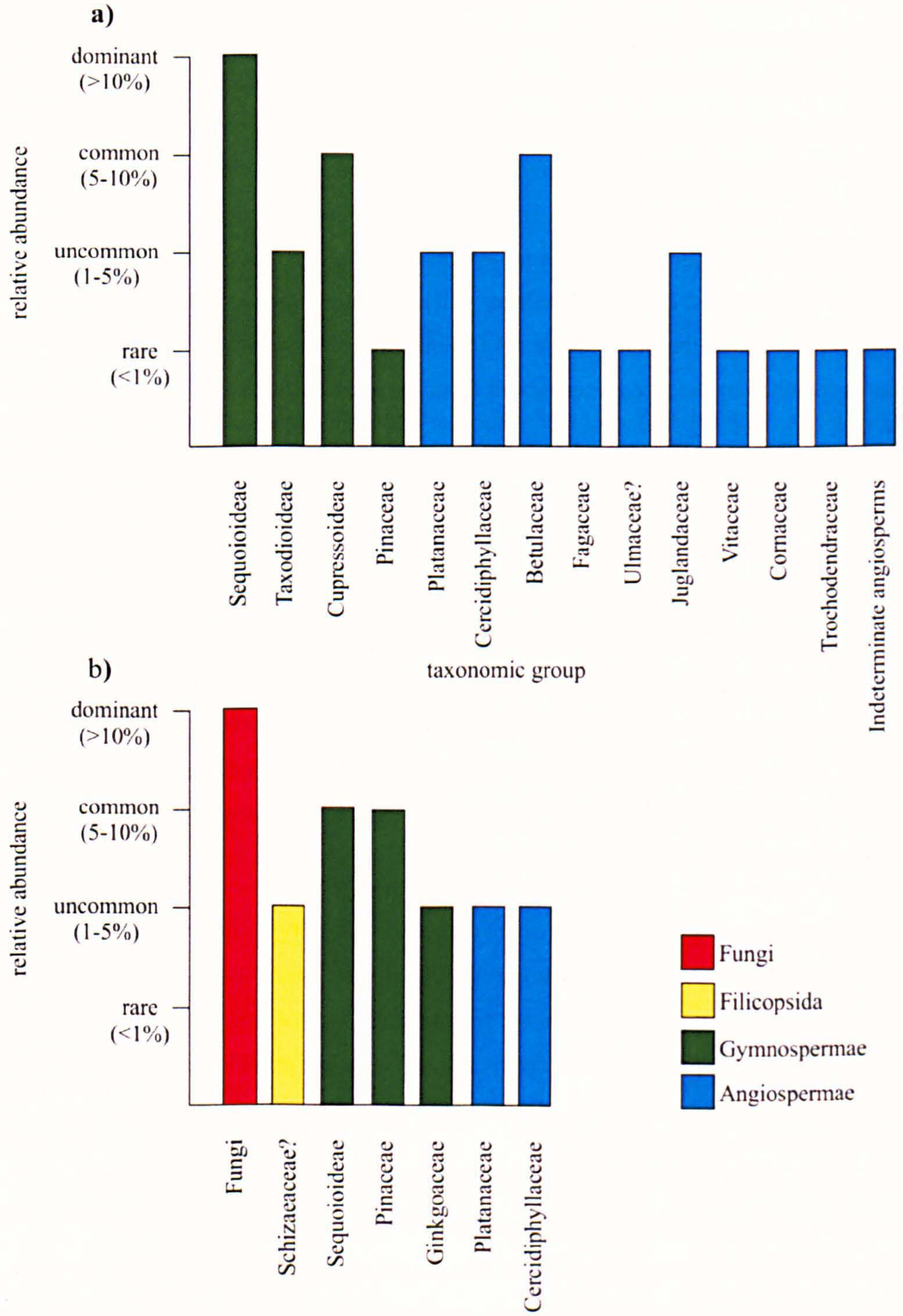

Figure 5.14. Comparison of family/subfamily diversity and relative abundance from a) macrofossils and b) microfossil assemblages of the Allt Mor flora of Skye. Palynological data from Jolley 1997.

The lack of correlation between the palynomorph and leaf record has important implications for the vegetation composition of the Allt Mor assemblage and the Paleocene vegetation as a whole. The Allt Mor assemblage has leaf taxa that are linked to a high proportion of the palynomorph taxa recorded from the Skye Lava Group (Tables 5.12 and 5.13). This indicates that the Allt Mor assemblage is highly representative of the Paleocene regional vegetation of Skye as it contains both local and more regional floral elements.

5.5 Vegetation reconstruction

5.5.1 Allt Mor

The depositional setting of the Allt Mor assemblage led to the accumulation of leaf material that originally grew in a variety of environments and communities (Figure 5.15). The Allt Mor assemblage includes vegetation with varied growth habits including climax canopy conifers, understory angiosperms, colonisers of disturbed habitats and a woody liana (Tables 5.6). Pollen and spores indicate that ferns and *Gingko* were present at Allt Mor (Jolley 1997).

The assemblage is dominated by Sequoioideae (*Sequoia* and *Metasequoia*), which collectively account for ~41% of the specimens within the collection. Their abundance suggests that they were the dominant elements of the vegetation. Pollen associated with these conifers is the most abundant component of the palynoflora, which supports the assertion they were ecologically-dominant trees at Allt Mor. Modern relatives of these conifers suggests that they represent the climax species in the community and would have formed tall canopy trees (Echenwalder 2009). The Sequoioideae conifers, particularly *Metasequoia*, may have been able to colonise the more disturbed sections of the floodplain because seedlings from the Paleocene of Alberta have shown that the trees were was capable of growing in these conditions (Falder et al. 1999).

The abundance of Cupressoideae conifers (collectively 7.7%) and *Corylites hebridicus* (7.7%) suggests these plants were ubiquitous elements of the vegetation. The Cupressoideae conifers were probably canopy trees of tall stature growing with Sequoioideae conifers in more stable conditions at the margins of the floodplain and on the valley sides. *Corylites hebridicus* was probably a short stature shrub or tree which was capable of growing under the canopy of these conifers, as well the more disturbed riparian environments (Figure 5.15). The possible liana, *Vitiphyllum sewardii*, grew amid the canopy conifers and understory shrubs and trees.

The other abundant angiosperm taxa, *Platanities hebridicus* (4.4%) and *Trochodendroides antiqua* (2.5%), may have grown in variety of environments. Their physiognomy indicates that they were well adapted to the shaded, humid conditions of the understory but their relatively high abundance and occurrence at Allt Geodh' a' Ghamhna and Glen Osdale indicates that they were capable of growing in disturbed riparian environments. These disturbed riparian environments would have supported angiosperm communities that included many of the angiosperm morphotypes of Allt Mor including; *Platanities hebridica*, *Trochodendroides antiqua*, *Corylites hebridca*, "*Corylites* cf.", *Cornophyllum hebridicum* and *Zizyphoides flabella* (Figure 5.15). The physiognomy of "*Platycarya* cf." indicates that it was a coloniser of disturbed environments and may have formed dense thickets along channels margins and floodplains (Figure 5.15).

The presence of an elevated water table and possible swamp development are indicated by the presence of *Glyptostrobus dunoyeri* and *Metasequoia occidentalis*, whose Paleogene and modern relatives are associated with water-logged conditions (LePage 2007, Greenwood and Basinger 1994). The palynological record of Allt Mor, Carbostbeg, a swamp deposit, indicate that juglandaceous angiosperms were abundant members of the swamp conditions of Skye (Jolley 1997). The rare morphotypes *Juglandiphyllites* sp.1 and sp.2 (AM 6-7) may have been juglandaceous representatives of swamp conditions at Allt Mor and grew in association with *Glyptostrobus* and *Metasequoia*.

Pinaceae pollen and needles indicate that pines grew in the more stable margins of the floodplain, valley sides and tops (Figure 5.15). The rarity of these macrofossil remains suggest that they were probably washed down from streams draining from the valley sides into the braided river channels where they were transported and deposited in the Allt Mor pond deposit. Other rare conifers such as *Mesocyapris* sp. and "*Calocedrus* cf.". may have grown in similar environments as the Pinaceae and owe their rarity to their distal location and winnowing through transport.

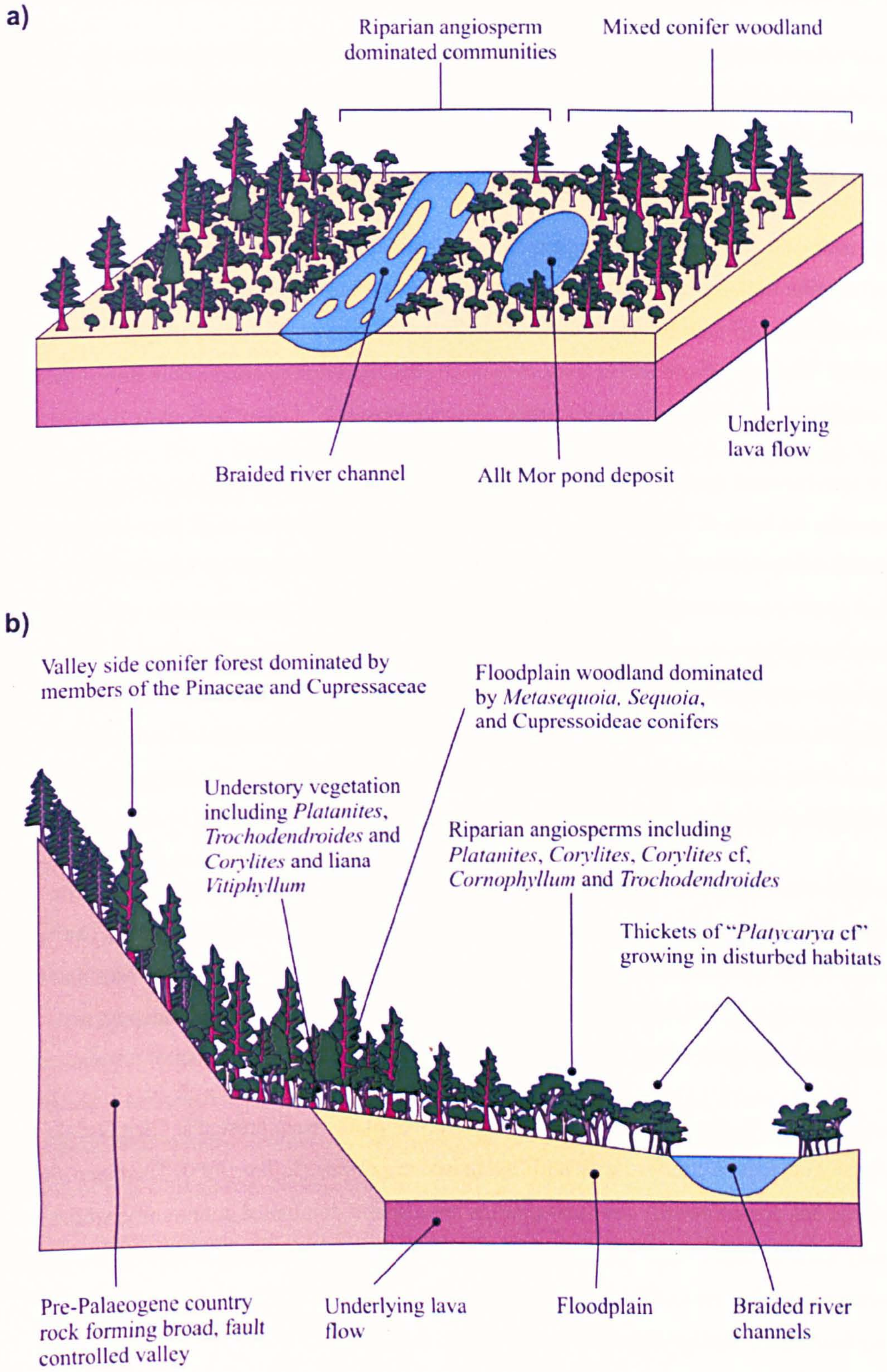

Figure 5.15. Paleoenviornmental and vegetation reconstruction of Allt Mor, Skye during the Paleocene. a) palaeoenvironments and local vegetation structure of the Allt Mor assemblage. b) Transect of the Allt Mor Member, showing palaeoenvironments and plant communities. Image not to scale.

5.5.2 Allt Geodh' a' Ghamhna and Glen Osdale assemblages

The plant macrofossil assemblages of Allt Geodh' a' Ghamhna and Glen Osdale are limited in terms of preservation and numbers of specimens so it is difficult to determine the original diversity and composition. Both sites do, however, share two features in common: they represent fluvial deposition and have yielded only angiosperm macrofossils.

The absence of conifer macrofossils from these assemblages is perhaps partly related to the limited number of specimens but could represent a true ecological signal. The coarser grain size of the sediments and their interpreted palaeoenvironment suggests disturbed floodplain deposition. The angiosperm leaves present at these sites represent riparian communities, which were capable of surviving in these disturbed environments.

Shared taxa between these sites are compared to Allt Mor to provide some insight into determining the habit of these plants. Two angiosperm taxa are present at all three localities and include *Corylites hebridicus* (AM3) and *Cornophyllum hebridica* (AM10). The former morphotype is a common component of the Allt Mor flora and its presence at the other localities suggests that it was a ubiquitous element of Skye, growing in both disturbed riparian settings, as well as in the more stable understory. *Cornophyllum hebridica* is a rare component of the Allt Mor flora but several specimens occur at both Allt Geodh' a' Ghamhna and Glen Osdale, so the presence of this morphotype in localities associated with higher intensity flooding suggests it favoured disturbed environments or was washed in from regional sites.

Three other angiosperm morphotypes present at Allt Mor occur at Glen Osdale and include *Platanites hebridicus* (AM1), *Trochodendroides antiqua* (AM3) and Morphotype 13. The presence of these taxa at Glen Osdale and their relative abundance at this site indicates that they represent riparian vegetation, although their physiognomy indicates they were adapted to understory conditions as well.

The pollen record, however, indicates a wider variety of plants were present at Glen Osdale including taxodiaceous conifer forest and Juglandaceae swamps (Jolley 1997). The macrofossil assemblage has preserved only the local riparian angiosperm dominated community, whilst regionally the vegetation cover was more heterogeneous. This is perhaps the case at Allt Geodh' a' Ghamhna, which is part of the same fluvial system as Allt Mor (Willaimson and Bell 1994), and may have had a similar vegetation composition as Allt Mor.

5.5.3 Regional vegetation reconstruction of Skye

The leaf and palynomorph assemblages from the interbasaltic sediments of the Skye Lava Group have provided important insights into the vegetation of this region during the mid Paleocene. Four broad community types are recognised: Pinaceae-dominated upland forest, mixed conifer forest, riparian angiosperm vegetation and juglandaceae/taxodiaceous swamp vegetation (Figure 5.16).

The pre-Paleogene landscape of Skye would have provided a more stable growth environment for vegetation development. These extra-basinal environments would have favoured the development of climax conifer forest (Figure 5.16). The pollen record indicates these upland environments were dominated by members of the Pinaceae, particularly in areas of greater elevation (Jolley 1997). Cupressaceous conifers may have grown amidst the pines, with ferns and angiosperms growing in the understory of these conifers.

Mixed coniferous forests appear to represent the climax vegetation in the more stable areas of upland and lowland settings as pollen produced by members of the Cupressaceae are widespread and often dominant (Jolley 1997). The Allt Mor macrofossil assemblage is dominated by members of this community type, such as Sequoioideae and Cupressoideae conifers and broad leaved angiosperms *Platanites*, *Trochodendroides* and *Corylites* (Figure 5.16). Tall stature conifers represent the climax canopy vegetation which may have been open in areas of disturbance or earlier stages of succession, but may have become progressively closed in more mature forests.

In areas of greater disturbance, such as channel margins and proximal floodplain settings, vegetation with adaptations to these environments would have been favoured (r-selected taxa). Angiosperms associated with the Platanaceae, Cercidiphyllaceae, Betulaceae, Ulmaceae?, Juglandaceae, Cornaceae and Trochodendraceae are present in both the macro and microfossil record and may have been well adapted to these conditions (Figure 5.16). These riparian angiosperm-dominated communities may have contained ferns and *Equisetum*, which are capable of colonising these conditions.

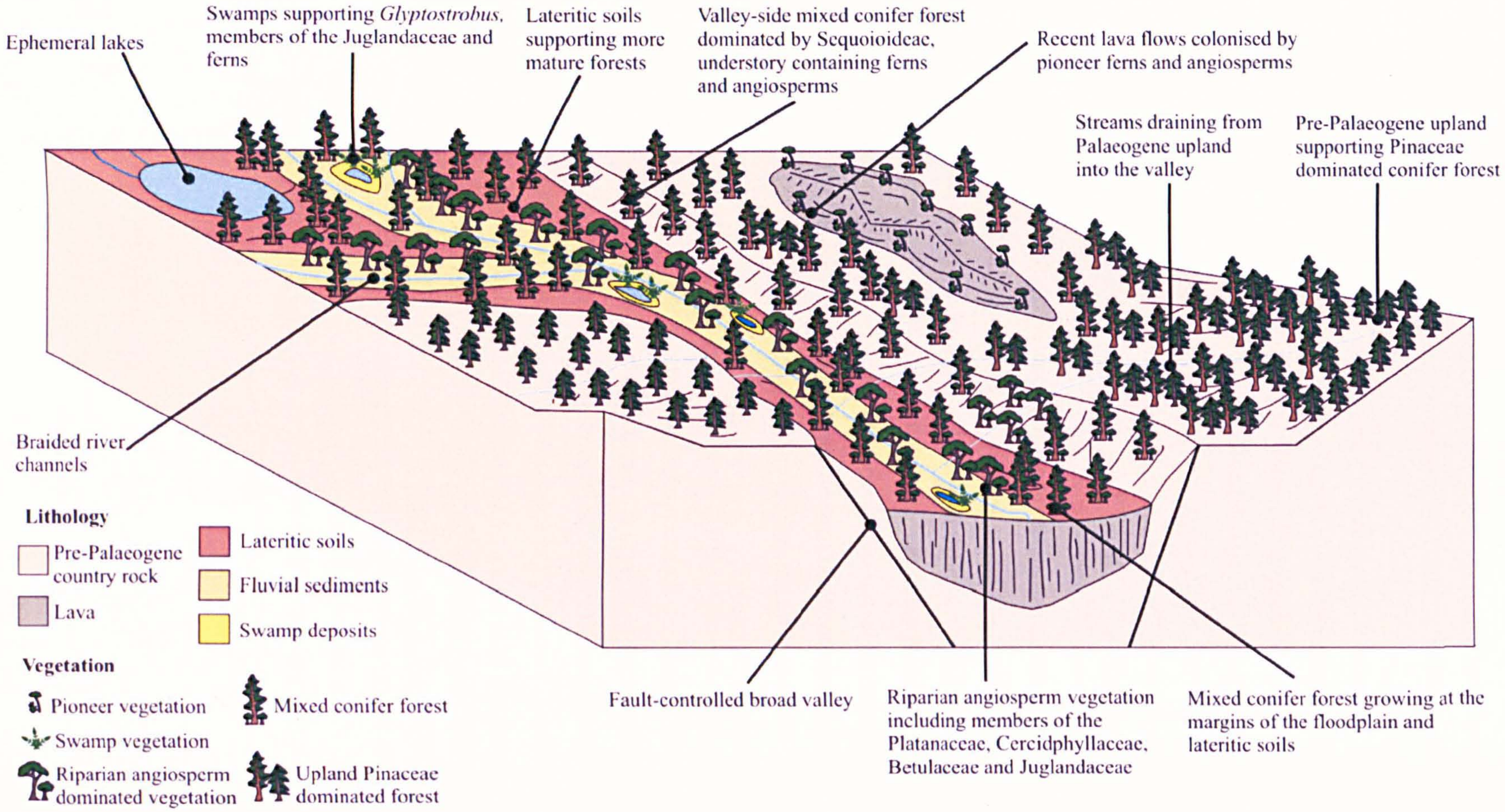

Figure 5. 5.16. Generalised schematic diagram of palaeoenvironments and vegetation of the Skye lava field during the Paleocene.

Thin coals and shale deposits provide evidence of elevated water-table and swamp development. Two palynological samples (Allt Mor, Carbostbeg and Tungadal River) represent swamp environments (Jolley 1997). Samples from these localities indicate there was considerable variability in the community structure of the swamp vegetation. Members of the Juglandaceae and taxodiaceaeous conifers appear to be the dominate members of these communities. Fern spores and angiosperm pollen indicates these communities were diverse and changed as drainage and stability increased (Jolley 1997) (Figure 5.16).

The lava fields, depositional environments and pre-Paleogene landscape of Skye during the mid Paleocene provided a range of environments for vegetation to colonise and develop. The palynomorph and macrofossil record suggests that the vegetation of Skye was dynamic and influenced by disturbance, water-level and topography. The initial colonisers of disturbed environments were the ferns and angiosperms but greater stability and maturation of these environments and communities enabled conifers to colonise and ultimately dominate the communities.

Chapter 6: Climate analysis of the Paleocene floras of Skye

6.1 Introduction

The floras of Skye present an opportunity to reconstruct the climate conditions of this region during the Paleocene. Presented in this chapter are the methods, results and discussion of the palaeoclimate analysis using the angiosperm leaf fossils from Skye. The methodology of physiognomic and nearest living relative approaches are outlined to demonstrate their use in estimating past climatic conditions. Results for each method are presented and discussed in light of potential limitations and biases inherent in each approach. The palaeoclimate data obtained from the analyses are then presented and used to decipher the climate signals encoded in the leaf fossils. Factors pertaining to botany, environment and taphonomy are discussed to evaluate their potential influences on the palaeoclimate signal. The climate results from the leaves are then compared with other geological proxies to interpret the past climate conditions of Skye during the mid Paleocene.

6.2 Palaeoclimate analysis

6.2.1 Introduction to palaeoclimatic methods

Plants are strongly influenced by climate. For plants to grow and reproduce successfully they have to be tolerant of the climate regime they occupy (Bailey and Sinnott 1915, 1916, Boyko 1947, Holdridge 1947, Huntley 1991). Longer lived plants such as woody dicotyledonous angiosperms have to be tolerant of the full range of climatic variations within a given area over annual, decadal or centennial timescales (Bailey and Sinnott 1915, Wolfe 1993). The taxonomic composition of floras and their morphological adaptations can provide important climatic signals, and have been used to reconstruct terrestrial palaeoclimates (e.g. Wing and Greenwood 1993, Wolfe 1993, Mosbrugger and Utescher 1997, Wilf 2000).

The morphology of leaves represents a trade-off between photosynthetic efficiency, tolerance of the ambient climatic conditions and the mechanical limitations of leaf construction (Spicer 2000). These constraints have led to the development of convergent leaf morphologies that are indicative of particular climates (physiognomy). The relationship between leaf physiognomy and climate has long been established since Bailey and Sinnott (1915, 1916) recorded the relationship between leaf margin type of woody dicotyledonous angiosperms (referred hereafter as woody dicots) and mean annual temperature (MAT). The research of Bailey and Sinnott (1915, 1916) showed that entire margined leaves (leaves with a smooth outer margin) are dominant in the humid tropics, and toothed leaves (leaves with tooth-like marginal projections) are prevalent in cooler, humid climates of the temperate regions. Since the early research by

Bailey and Sinnott (1915, 1916) physiognomic methods have developed significantly and are outlined in sections 6.2.3 to 6.2.5

The composition of floras is often related to the specific climatic conditions because through their evolutionary history plant groups have become adapted to specific climatic ranges (Mossbrugger and Utescher 1997). The taxonomic composition of a fossil flora can therefore provide signals of past climates if their modern relatives are restricted or characteristic of specific climatic ranges. The application and potential of this method in this study is outlined in sections 6.2.6.

6.2.2 Scoring of physiognomic characters

The physiognomy of each of the fossil woody dicot leaf morphotypes from Skye were scored for the climate analysis. The margin type of each morphotypes was determined by the presence or absence of teeth. Leaves that posses teeth receive a score of 1 (toothed) and those without receive a score of 0 (entire). The presence of a single tooth on leaf is sufficient to score it as toothed. Entire margined leaves, however, require a more complete margin to be scored. Individual leaves or leaf morphotypes that lack any marginal preservation are not scored for this leaf character. The margin type of the Allt Mor morphotypes are presented in section 6.3.1 (Table 6.2).

Scoring for multivariate physiognomic approaches such as Climate Leaf Analysis Multivariate Program (CLAMP) and Multiple Linear Regression Models (MLR) requires the correct identification and scoring of multiple leaf character traits. Thirty one leaf character traits were scored in this study and are based on those outlined in Wolfe (1993) and Kovach and Spicer (1995). A detailed description with figured examples of these 31 character states and how to score them is present on the CLAMP website (http://clamp.ibcas.ac.cn). The 31 leaf characteristics represent either discontinuous traits that are scored as being present or absent, or are continuous traits and require measurements to accurately score them. Continuous physiognomic characters used in this study include lamina size and lamina length:width ratios. These traits were measured for leaves complete enough for each morphotype using ImageJ software, the procedure for which is presented in Chapter 3, section 3 3.5.6. Leaves that are fragmented but retain enough lamina preservation to estimate their size and length:width ratio were estimated (See Chapter 3, section 3 3.5.6). Estimates of lamina size and length:width ratio were only used if they did not potentially overlap two categories (e.g. microphyll I and microphyll II). The combined percentage score for all 31 characters for the Skye flora is presented in section 6.3.1 (Table 6.4).

6.2.3 Leaf margin analysis (LMA)

The relationship between the leaf margin of woody dicot species and mean annual temperature (MAT) has been a focus of scientific study since Bailey and Sinnott (1915, 1916) recognised the strong correlation between the percentage of entire margin leaves within a flora and MAT. Wolfe (1979) was the first to quantify the relationship of entire margin percentage and MAT by correlating the percentage of entire margin leaf species from the floras of East Asia with the MAT of those sites from climate stations.

The correlation between margin percentage and MAT from the floras of East Asia was highly significant ($p = <0.001$) with an r^2 value of 0.98 (Wing and Greenwood 1993). The study by Wolfe (1979) showed that a 3% increase in the number of entire margined species within a flora equates to a 1°C increase in MAT. Wing and Greenwood (1993) were able to establish the correlation and transfer function from the Wolfe (1979) dataset for the use in palaeoclimatic studies (Figure 6.1 and Table 6.1).

This univariate model was termed Leaf Margin Analysis (LMA) and has provided robust measures of terrestrial MAT for the Cenozoic (e.g. Wolfe 1979, Wing and Greenwood 1993). The strong correlation between the percentage of margin type and MAT has been recognised in other regions (Table 6.1), which indicates that this correlation is robust across the Northern Hemisphere. Seven LMA equations have been selected in this study (Table 6.1) because they represent primarily Northern Hemisphere floras and climates, and are therefore likely to share similar characteristics with the Skye fossil floras.

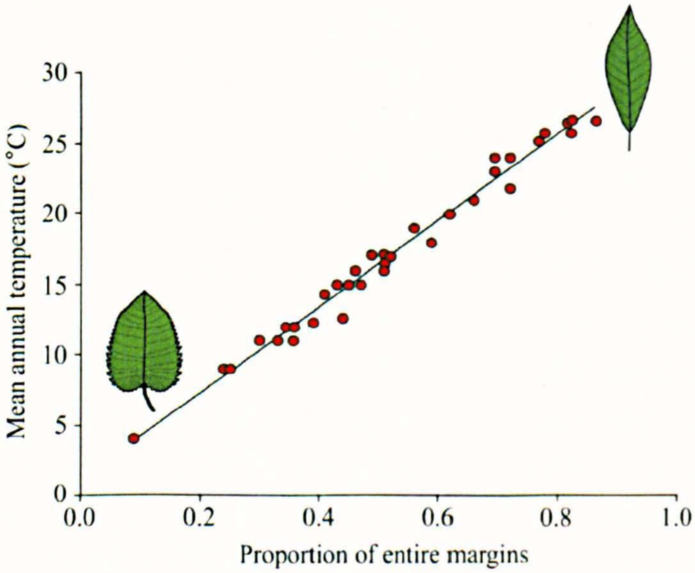

Figure 6.1. Correlation between mean annual temperature and proportion of entire-margined species in floras from East Asia, data set of Wolfe (1979). Each data point represents a single modern flora with multiple constituent woody dicotyledonous angiosperm species. Redrawn and modified from Wing and Greenwood (1993).

Table 6.1. Leaf margin analysis transfer functions used in this study from datasets derived from different regions.

Transfer function	Region	r^2	n	SE	Authors
(1) MAT = 1.141 + 30.6 x P	East Asia	0.98	34	0.8	(Wolfe 1979, Wing and Greenwood 1993)
(2). MAT = 2.240 + 28.6 x P	North, Central and South America	0.94	9	2	(Wilf 1997)
(3). MAT= -0.266 + 29.1 x P	North and Central America and Japan	0.76	106	3.4	(Wilf 1997)
(4). MAT = 2.223 + 36.3 x P	North America	0.8	16	3.6	(Kowalski and Dilcher 2003)
(5). MAT = 0.512 + 31.4 x P	Europe	0.6	1835	1.7	(Traiser et al. 2005)
(6). MAT = 1.320 + 29 x P	North and Central America	0.91	84	NA	(Miller et al. 2006)
(7). MAT = 1.038 + 27.6 x P	China	0.79	50	1.9	(Su et al. 2010)

Numbers in parentheses e.g. (1) – (7) denote the different LMA transfer functions used in this study. MAT = mean annual temperature, P = proportion of woody dicots with entire margins, r^2 = strength of the correlation, n = number of sites sampled, SE = standard error.

6.2.4 Climate Leaf Analysis Multivariate Program (CLAMP)

Climate Leaf Analysis Multivariate Program (CLAMP), unlike LMA, is a multivariate statistical approach that uses multiple leaf characters to decipher the climate from leaf physiognomy (Wolfe 1993). This technique determines the relationship between the physiognomy of woody dicot leaves and meteorological variables of modern terrestrial environments (Figure 6.2). The relationship between modern leaf physiognomy and meteorological data can then be applied to fossil leaf assemblages to determine past climatic conditions. CLAMP, unlike LMA, is able to determine not only MAT but also other climate variables related to seasonality and precipitation (Wolfe 1993).

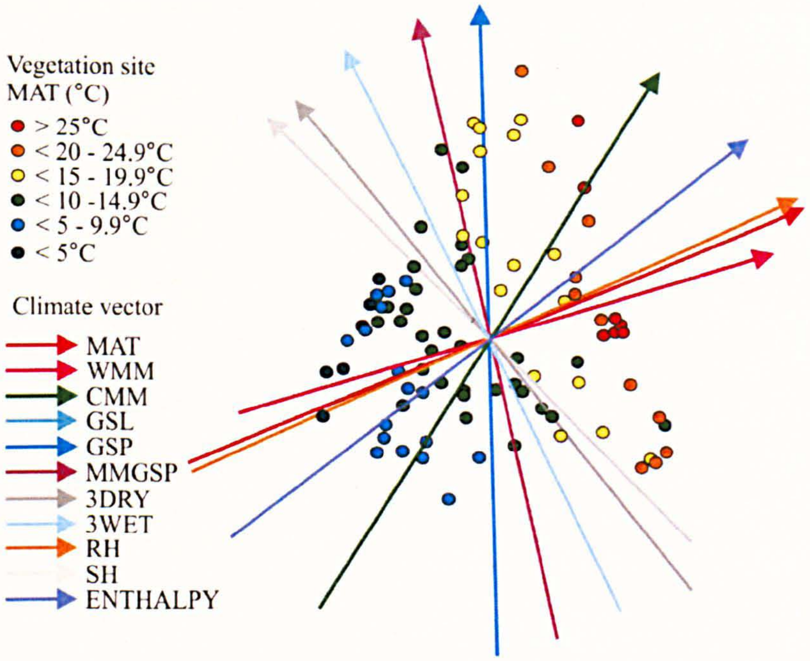

Figure 6.2. Example of multidimensional relationship between the physiognomy of floral sites and climate. Redrawn from the CLAMP website (http://clamp.ibcas.ac.cn).

CLAMP as a technique is useful, particularly for older floras, as the taxonomic identity of the leaves is not required, rather the analysis relies on the convergence of physiognomic traits between plant taxa (Spicer 2000). However, angiosperm leaf morphotypes have to be correctly identified and characterised prior to the analysis, and their full range of physiognomic variation determined. Once the angiosperm morphotypes have been established (see Chapter 3 for procedure) they are scored for the CLAMP analysis. CLAMP uses 31 leaf characters that are related to lobation, margin, lamina size, apex and base shape, lamina shape and length:width ratio. For details on scoring and definition of these characters see http://clamp.ibcas.ac.cn. The combined score for all morphotypes within the fossil flora is then matched against the modern floras and meteorological data using Canonical Correspondence Analysis (CANOCO) statistical software (Ter Braak 1986), and now can be run via the CLAMP website (http://clamp.ibcas.ac.cn). CANOCO ordinates the physiognomic and meteorological data (simplifies the variables) to determine their relationship, which can then be applied to fossil floras.

The current CLAMP calibration dataset consists of 173 modern sites (Physg3arcAZ), mostly from the Northern Hemisphere. Each site represents an individual flora composed of more than 20 woody dicots whose physiognomy has been recorded along with the local climate from climate observations of greater than 30 years. A second calibration dataset is available, which excludes the cold 'alpine-nest' sites (Physg4brcAZ). The use of this dataset is applicable if initial results indicate a warm palaeoclimate, but in this study both physiognomic datasets have been used to establish which dataset is most comparable with the other methods.

The meteorological data is available in two formats; the first is derived from >30 year averages from individual climate stations, the second dataset is derived from globally gridded climate. These datasets enable four analyses to be performed-two analyses that utilises the full 173 sites with gridded climate data (CLAMP1), meteorological data (CLAMP2), and two analyses that use the reduced floral dataset (excluded cold sites) with gridded climate data (CLAMP3), and meteorological data (CLAMP4). All four analyses have been used in this study to firstly test the variability of each analysis and secondly to establish which provides the most congruent results with the other methods used.

6.2.5 Multiple linear regression models (MLRs)

Multiple linear regression models (MLRs) represent another application of multivariate physiognomic data for palaeoclimate analysis. Several MLRs have been derived from the CLAMP calibration datasets, but do not rely on ordination from CANOCO. Instead, regression analysis of the predictor variables (physiognomic characters) and dependant variables (climate variables) are calculated using the linear regression models. Three MLR models based on the CLAMP calibration datasets have been used in this study. All utilise the complete or selected leaf character states outlined by Wolfe (1993), for specific details on definition of scores see (http://clamp.ibcas.ac.cn). The three MLR models used in this study are presented below:

a. MLR1 model is derived from the Wing and Greenwood (1993) who used 74 sites from the CLAMP database and excluded sites with cold month mean temperature < -2°C. This model eliminated many of the 31 characters used in CLAMP to reduce multicollinearity (strong linear correlation between two or more dependent variables). A single character from each leaf form category (e.g. margin characters, lamina shape etc.) was selected according to two criteria; a low correlation with other character states to reduce multicollinearity, and a high correlation between the physiognomic character and a specific climatic variable (Wing and Greenwood 1993, Wiemann et al. 1998).

b. MLR2 model is derived from Gregory and McIntosh (1996) and uses 106 sites from the CLAMP dataset and 29 of the 31 physiognomic characters. The 'teeth close' and 'teeth regular' characters were excluded due to their close correlation with (collinearity) the 'no teeth' (entire margined) character (Gregory and McIntosh 1996). The character states used are presented in Table 6.2 and are defined and scored according to the CLAMP guidelines (see http://clamp.ibcas.ac.cn).

c. MLR3 model is derived from Wiemann et al. (1998) and represents untransformed data from 144 sites from the CLAMP database. All 31 character states were used. The MLR model produced by Wiemann et al. (1998) selected the leaf characters most strongly correlated with MAT and growing season precipitation (GSP).

6.2.6 Nearest living relatives (NLRs)

This approach relies not on the physiognomic attributes of the fossil plants to reconstruct the past climate but the systematic relationship of the modern relatives and their climatic tolerances. The use of nearest living relatives (NLRs) as climate proxies for fossil assemblages is an established method for estimating past climates (e.g. Heer 1855, Greenwood and Wing 1993, Mosbrugger and Utescher 1997, Uhl et al. 2007). This approach requires that the systematic identity of the plant is accurately determined and the fossil plant has to have a modern relative, preferably a close one, with a well documented climate range (Mosbrugger and Utescher 1997).

The coexistence approach developed by Mosbrugger and Utescher (1997) uses the principal of NLRs but also uses the coexistence of taxa i.e. the range where all taxa overlap for a particular climate variable (Figure 6.3). This point of coexistence for the modern relatives is used as the estimate of that particular climate variable for the fossil plant assemblage.

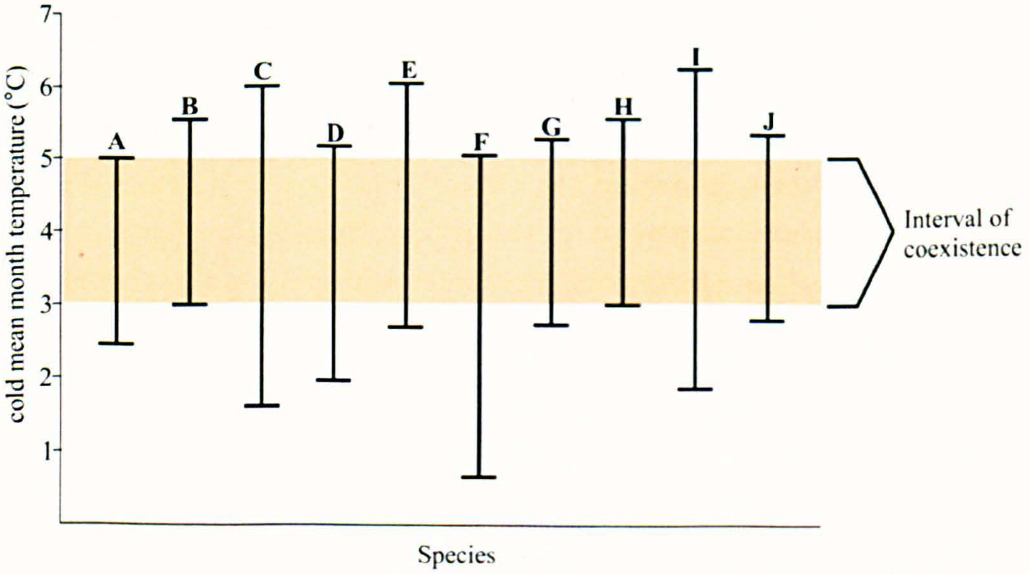

Figure 6.3. Demonstration of coexistence approach. Plant species A-J represent modern relatives of fossil taxa. Each plant species has a range of cold mean month temperatures they can tolerate. The shaded orange area represents the interval of coexistence where theoretically all taxa could coexist, in this example 3 °C to 5 °C.

6.3 Results

6.3.1 Mean annual temperature estimates derived from leaf margin analysis (LMA)

The fossil woody dicot leaves of Allt Mor, Skye are dominated by morphotypes with toothed margins (Table 6.2). Of the twelve morphotypes with margin preserved only one, *Cornophyllum hebridicum* (AM 10) has an entire margin. The percentage of leaf morphotypes within the Allt Mor flora with entire margins is 8.3%. This percentage was converted to a proportion of the flora (0.083) and applied to the LMA equations presented in Table 6.1 to determine MAT, the results of which are presented in Table 6.3.

Table 6.2. Margin type of the angiosperm morphotypes of Allt Mor, Skye.

Morphotype	Toothed margin	Entire margin
AM1 *Platanites hebridicus*	X	
AM2 *Trochodendroides antiqua*	X	
AM3 *Corylites hebridicus*	X	
AM4 "*Corylites* cf."	X	
AM5 *Fagopsiphyllum groenlandica*	X	
AM6 *Juglandiphyllites* sp.1	?	?
AM7 *Juglandiphyllites* sp.2	X	
AM8 "*Platycarya* cf."	X	
AM9 *Vitiphyllum sewardii*	X	
AM10 *Cornophyllum hebridicum*		X
AM11 *Zizyphoides sp.*	X	
AM12 affinity unknown	X	
AM13 affinity unknown	X	
AM14 affinity unknown	?	?

AM = angiosperm morphotype, X = denotes margin type, ? = margin not preserved.

Table 6. 6.3. Mean annual temperature estimates of the mid Paleocene of Skye, derived from seven LMA equations

Leaf margin analysis transfer function	Mean annual temperature (°C)	Standard error ('sampling error') (± °C)
LMA (1)	3.7	2.4
LMA (2)	4.6	2.3
LMA (3)	2.2	2.3
LMA (4)	5.2	2.9
LMA (5)	3.1	2.5
LMA (6)	3.7	2.3
LMA (7)	3.3	2.2

Numbers in parentheses denote LMA transfer function used, see table 6.1 for the source. Standard error calculated from Wilf (1997).

The standard error for each LMA equation was calculated according to the calculation presented in Wilf (1997) and is presented below.

$$\sigma\,(MAT) = \frac{\sqrt{P(P-1)}}{r}$$

where c refers to the slope of the correlation of the transfer function e.g. 30.6 for LMA (1) and 28.6 for LMA (2) etc. P is the proportion of leaf morphotypes within the flora with entire margins, in this case 0.083. r is total number of leaf morphotypes used in the analysis, in this case 12. The calculated sampling error for each of the seven LMA transfer function equations is presented in Table 6.3.

The calculation determined by Wilf (1997) yields the sampling error, which is typically greater than the standard error published in the original studies (see Table 6.1). Sampling error diminishes with greater number of species/morphotypes incorporated into the analysis or if the margin percentage is skewed e.g. 20% or 80%. The Allt Mor flora has only 12 morphotypes with margin preserved and should therefore have high sampling error, but because margin percentage is low at 8.3% it yields a standard error ranging from ~2 °C to 3 °C (Table 6.3). The standard error obtained from the Allt Mor flora is greater than all but two of the published standard errors for each equation (see Tables 6.1 and 6.3) but is around the minimum suggested by Wilf (1997) for MAT estimates derived from LMA.

The MAT estimates derived from the seven LMA equations indicate a possible range of MAT of 2.2 ± 2.3 °C to 5.2 ± 2.9 °C (Table 6.3) during the mid Paleocene of Skye error taken into account the maximum range is -0.1 °C to 8.1 °C. The mean of all of the estimates is 3.7 °C, which is suggestive of a cold temperate climate (Wolfe 1979). Three of the results appear to depart significantly from this mean including LMA (2), LMA (3) and LMA (4) (Table 6.3). The implications of these possible estimate outliers are discussed in section 6.4.4.

6.3.2 Climate estimates derived from CLAMP analysis

The physiognomic characters scored for the Allt Mor indicates the flora is dominated by unlobed, toothed leaf types, leaves with round teeth, leaves of microphyll III to mesophyll I size, leaves with acute and attenuate apexes, all base shapes, particularly acute, lamina length:width ratios of 1-2:1 to 2-3:1 and elliptic laminas. A completeness score of 0.6 was obtained from this flora. This completeness score equates to relative number of characters that have been scored for the flora. The calibration dataset floras (modern floras) have a completeness of score 1, i.e. 100% of the characters for each leaf species within the flora has been scored. Low completeness scores indicate fewer of the characters have been scored. Spicer et al. (2005) suggest that a completeness score of 0.6 should be minimum for reliable climates estimates derived from CLAMP.

The completeness score for the Skye floras is therefore at the minimum required for reliable estimates when using CLAMP. This low completeness score is due to the limited preservation of several of the morphotypes, particularly morphotypes AM4 and M12-M15. These morphotypes were included in the analysis to provide the full range of physiognomic characters represented in the Allt Mor flora and to reduce the effects of limited diversity.

Four versions of the CLAMP analysis were performed in this study and the predicted climate estimates are presented in Table 6.5. The standard error for each of the climate variables was generated by the analysis and are presented in Table 6.5.

Table 6.4. Leaf physiognomic characters scored for the Allt Mor flora.

leaf character	percentage	leaf character	percentage
lobed	0	apex shape: emarginate	0
no teeth (entire margin)	8	apex shape: round	14
teeth regular	50	apex shape: acute	43
teeth close	50	apex shape: attenuate	43
teeth round	63	base shape: cordate	27
teeth acute	29	base shape: round	27
teeth compound	25	base shape: acute	45
lamina size: nanophyll	0	lamina length:width <1:1	22
lamina size: leptophyll I	0	lamina length:width 1-2:1	33
lamina size: leptophyll II	0	lamina length:width 2-3:1	39
lamina size: microphyll I	7	lamina length:width 3-4:1	6
lamina size: microphyll II	7	lamina length:width >4:1	0
lamina size: microphyll III	52	lamina shape: obovate	4
lamina size: mesophyll I	19	lamina shape: elliptic	96
lamina size: mesophyll II	10	lamina shape: ovate	0
lamina size: mesophyll III	6		

For definitions of these character states see the CLAMP website (http://clamp.ibcas.ac.cn).

Table 6.5. CLAMP predicted climatic variables derived from the physiognomy of the Allt Mor flora.

calibration dataset	MAT (°C)	SE	CMM (°C)	SE	WMM (°C)	SE	GSL (months)	SE	GSP (mm)	SE	MMGSP (mm)	SE	3WET (mm)	SE	3DRY (mm)	SE
Physg3arc_GridMet (CLAMP1)	10.3	1.7	0.0	3.0	20.8	1.8	6.3	0.8	1380.1	193.8	202.0	24.7	828.2	132.9	266.5	35.5
Physg3arc_Met (CLAMP2)	10.9	1.8	1.6	2.6	20.8	1.8	6.8	0.9	1721.7	317.3	242.0	37.0	892.7	137.3	602.7	89.4
Physg3brc_GridMet (CLAMP3)	11.1	1.1	0.5	1.9	22.2	1.4	6.7	0.7	1409.2	200	208.1	26.3	741.0	146.5	261.2	31.7
Physg3brc_Met (CLAMP4)	11.7	1.2	1.6	1.9	22.8	1.6	7.1	0.7	1742.2	330.8	249.5	31.4	910.4	140.8	665.8	104.3

Calibration datasets used: Physg3arc_GridMet (CLAMP1) = 173 floral sites with gridded climate data, Physg3arc_Met (CLAMP2) = 173 floral sites with climate observation data, Physg3brc_GridMet (CLAMP3) = 144 floral sites with gridded climate data, Physg3brc_Met (CLAMP4) = 144 floral sites with climate observation data. SE = standard error, MAT = mean annual temperature, CMM = cold month mean temperature, WMM = warm month mean temperature, GSL = growing season length, MMGSP = mean monthly growing season precipitation, 3WET = three wet month precipitation, 3DRY = three dry month precipitation.

The predicted climate parameters from the four CLAMP analyses indicate a warm, seasonal climate with high precipitation (Wolfe 1993). The four analyses used in this study show significant variation in the minimum, maximum, mean and total range of the estimates produced (Table 6.6).

Table 6.6. Climate variables derived from the four CLAMP analyses showing minimum, maximum, mean and range of estimates.

Climate variable	min	max	mean	range
(MAT) mean annual temperature (°C)	8.6	12.9	11.0	4.3
(CMM) cold mean month temperature (°C)	-3.0	4.2	0.9	7.2
(WMM) warm mean month temperature (°C)	19.0	24.4	21.6	5.4
(GSL) growing season length (months)	5.5	7.8	6.7	2.3
(GSP) growing season precipitation (mm)	1186.3	2073.0	1563.3	886.7
(MMGSP) mean monthly growing season precipitation (mm)	177.3	280.9	225.4	103.7
(3WET) three wet month precipitation (mm)	695.4	1051.2	843.1	355.9
(3DRY) three dry month precipitation (mm)	231.1	770.1	449.1	539.0

Mean annual temperature estimates range from 10.3 ± 1.7 °C to 11.7 ± 1.2 °C and with the standard error taken into account the potential range is 8.6 °C to 12.9 °C with a mean of 11 °C for the four estimates (Table 6.5, 6.6). These mean annual temperature estimates suggest that the climate was temperate to warm temperate (Wolfe 1993). Cold month mean temperature (CMM) estimates range from 0.0 ± 3 °C to 1.6 ± 2.6 and with the standard error taken into account have a range of -3.0 °C to 4.2 °C with a mean of 0.9 °C (Table 6.5, 6.6). The estimates for CMM show the greatest range between the four analyses but suggest that winter temperatures were cool, and frosts may have been frequent. Warm month mean temperature (WMM) estimates range from 20.8 ± 1.8 °C to 22.8 ± 1.6 °C. The maximum range in estimates of WMM with the standard error taken into account is 19.0 °C to 24.4 °C with a mean of 21.6 °C (Table 6.5, 6.6).

Precipitation estimates indicate a humid climate state, but estimates derived from the four CLAMP analyses show significantly more variation than the temperature-related climate parameters (Table 6.6). Growing season precipitation (GSP) estimates range from 1380.1 ± 193.8 mm to 1742.2 ± 330.8 mm (Table 6.5, 6.6). The total range between the estimates for GSP is 886.7mm (Table 6.6), which indicates the reliability of this climate parameter is limited. This pattern is also apparent in the mean monthly growing season precipitation (MMGSP), three wet month precipitation (3WET) and three dry month precipitation (3DRY) (Table 6.6). The level of precipitation is therefore obscured by the high standard error of these of these parameters and the variance between the estimates.

The four CLAMP analyses in this study as outlined in section 6.2.4 are derived from datasets with varying numbers of floral sites and different source climate data. There is a discrepancy between the analyses that are based on the gridded climate data (CLAMP1 and CLAMP3) and those that are based on meteorological observations (CLAMP2 and CLAMP4) (Table 6.5). Precipitation estimates derived from the gridded climate datasets are appreciably drier than the meteorological observations (Table 6.5). This is consistent with the findings of Spicer et al. (2009) who showed that the gridded dataset yielded drier estimates compared to the meteorological observations. This discrepancy is caused by the climate models, (that produced the gridded data) inability to determine fine scale precipitation patterns such as storm events, which the meteorological observations have recorded (Spicer et al. 2009).

The estimates obtained from the full floral dataset (CLAMP1 and CLAMP2) and those derived from the reduced dataset (CLAMP3 and CLAMP4) show a slight discrepancy in the temperature related parameters (Table 6.5). This discrepancy is expected as the reduced dataset has had the colder sites removed and so yields warmer temperature estimates, but, as the estimates show, this difference is slight.

6.3.3 Climate estimates derived from MLR models

The three MLR models used in this study have produced highly variable estimates of the climate, particularly CMM and mean annual range in temperature (MART) (Tables 6.7, 6.8). The standard error for each of the climate variables was obtained from their source publication (Table 6.7), except for MAT which was calculated using the methodology outlined by Wilf (1997).

Table 6.7. MLR predicted climate variables from the physiognomy of the Allt Mor flora.

MLR model	MAT (°C)	SE	CMM (°C)	SE	WMM (°C)	SE	MART (°C)	SE	GSP (mm)	SE
MLR1	3.4	2.0	-7.6	3.6	20.0	2.9	16.8	5.0	1794.7	472
MLR2	0.1	2.3	-14.8	3.5	23.3	2.5	30.9	3.8	1475.6	300
MLR3	5.5	2.0	-	-	-	-	-	-	1705.1	512

MLR models used MLR1 = Wing and Greenwood (1993), MLR2 = Gregory and McIntosh (1996), MLR3 = Wiemann et al. (1998). MAT = mean annual temperature, SE = standard error, CMM = cold mean month temperature, WMM = warm mean month temperature, MART = mean annual range in temperature, MAP = mean annual precipitation, GSP = growing season precipitation. - = transfer function not available to determine this particular climatic variable.

Table 6.8. Climate variables derived from the three MLR models showing minimum, maximum, mean and range of estimates.

Climate variable	min	max	mean	range
(MAT) mean annual temperature (°C)	-2.2	7.5	3	9.7
(CMM) cold mean month temperature (°C)	-18.3	-4	-11.2	14.3
(WMM) warm mean month temperature (°C)	17.1	25.8	21.7	8.7
(MART) mean annual range in temperature (°C)	11.8	34.7	23.9	22.9
(GSP) growing season precipitation (mm)	1175.6	2266.7	1658.5	1091.1

Mean annual temperature estimates from the three MLR models are highly variable and range from 0.1 ± 2.3 °C to 5.5 ± 2.0 °C, and with standard error taken into account the maximum range is -2.2 °C to 7.5 °C with a mean of 3 °C (Tables 6.7, 6.8). The estimates of MAT derived from all three MLR models indicate temperate to cool temperate climate state (Wolfe 1979). Estimates of CMM are very low and range from 7.6 ± 3.6 °C to -14.8 ± 3.5 °C and with standard error the maximum range is -4 °C to -18. 3°C with a mean of -11.2 °C (Tables 6.7, 6.8). These CMM estimates suggest the winter temperatures on Skye during the mid Paleocene were severe and hard frosts were frequent. The two estimates for WMM are more comparable and range from 20 ± 2.9 °C to 23.3 ± 2.5 °C and with standard error the maximum range is 17.1 °C to 25.8 °C with a mean of 21.7 °C (Tables 6.7, 6.8).

The mean annual range in temperature (MART) estimates produced from MLR1 and MLR2 vary significantly (Tables 6.7, 6.8). The estimates range from 16.8 ± 5 °C to 30.9 ± 3.8 °C and with standard error taken into account the range is 11.8 °C to 34.7 °C with a mean of 23.9 °C (Tables 6.7, 6.8). Estimates of MART derived from the MLR1 model indicate that there was a lower annual range in temperature, which is supported by the relatively warmer CMM estimates and cooler WMM estimates. The MLR2 model, however, indicates that the annual range in the temperature was much greater which is supported by the CMM and WMM estimates from this model.

Estimates of GSP vary significantly and range from 1475.6 ± 300 mm to 1794.7 ± 472 mm, and with the standard error range from 1175.6 mm to 2266.7 mm with a mean of 1658.5 mm (Tables 6.7, 6.8). The MLR estimates of GSP, like CLAMP, have high range between the estimates (1091.1 mm), which indicates that this climate perimeter is poorly constrained.

Although the three MLR models have predicted a greater variation of estimates compared to CLAMP they show similar trends, which indicate the climate during the Paleocene of Skye was cool temperate, strongly seasonal with warm summers and severe winters and humid during the growing season.

6.3.4 Nearest living relatives approach

The use of NLRs as climate indicators has not been implemented in this study for several reasons, which are outlined below:

a. The potential for the modern relatives of the Skye floras to have changed their climatic tolerances is high after ~60 million years of evolution and Cenozoic climate change.

b. Many of the conifer taxa on Skye have modern relatives that have restricted, relict distributions such as *Metasequoia*, *Sequoia* and *Glyptostrobus* (Eckenwalder 2009). The Paleocene record of these conifers, however, indicates that they had a much broader latitudinal and longitudinal ranges, and therefore broader climate tolerances than their extant relatives (Liu et al. 2007, LePage 2007).

c. The angiosperm leaf morphotypes of Skye can only be identified to family level with any degree of confidence. At such high taxonomic levels the accuracy of any estimates is likely to be limited.

d. Paleocene angiosperms in many cases represent archaic, undifferentiated forms that share morphologically characters with extinct and extant genera (Manchester 1999). The climate tolerances based on their NLRs are difficult to ascertain as they may have tolerances similar to one, or several of the genera.

Because of these factors the use of NLRs as climate proxies for the mid Paleocene of Skye suggests that the climatic estimates produced may be unreliable and of limited accuracy. The NLRs for the Skye floras will be considered in this study but only as qualitative palaeoecological and palaeoclimatic indicators.

6.3.5 Summary of results

Fourteen separate analyses have been performed in this study, which represent three forms of physiognomic climate analysis: LMA, CLAMP and MLRs. The climate variables that have been estimated by these analyses have provided climate signals for the mid Paleocene of Skye (Table 6.9). These estimates do, however, show significant variation (Table 6.9), the source of this variation is discussed in the following section 6.4.

Table 6.9. Climate estimates derived from the physiognomic analysis of the mid Paleocene floras of Skye using LMA, CLAMP and MLR models.

Model	MAT (°C)	SE	CMM (°C)	SE	WMM (°C)	SE	MART (°C)	SE	GSL (months)	SE	GSP (mm)	SE	MMGSP (mm)	SE	3WET (mm)	SE	3DRY (mm)	SE
LMA1	3.7	2.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA2	4.6	2.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA3	2.2	2.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA4	5.2	2.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA5	3.1	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA6	3.7	2.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA7	3.3	2.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CLAMP1	10.3	1.7	0.0	3.0	20.8	1.8	-	-	6.3	0.8	1380	194	202	25	828	133	267	35
CLAMP2	10.9	1.8	1.6	2.6	20.8	1.8	-	-	6.8	0.9	1722	317	242	37	893	137	603	89
CLAMP3	11.1	1.1	0.5	1.9	22.2	1.4	-	-	6.7	0.7	1409	200	208	26	741	146	261	32
CLAMP4	11.7	1.2	1.6	1.9	22.8	1.6	-	-	7.1	0.7	1742	331	250	31	910	141	666	104
MLR1	3.4	2.0	-7.6	3.6	20.0	2.9	16.8	5.0	-	-	1795	472	-	-	-	-	337	89
MLR2	0.1	2.3	-14.8	3.5	23.3	2.5	30.9	3.8	-	-	1476	300	-	-	-	-	-	-
MLR3	5.5	2.0	-	-	-	-	-	-	-	-	1705	512	-	-	-	-	-	-

MAT = mean annual temperature, SE = standard error, CMM = cold mean month temperature, WMM = warm mean month temperature, MART = mean annual range in temperature, GSL = growing season length, GSP = growing season precipitation, MMGSP mean monthly growing season precipitation, 3WET = three wet month precipitation, 3DRY = three dry month precipitation, - = transfer function not available to determine this particular climatic variable.

6.4 Discussion of results

Climate estimates derived from the physiognomy of the angiosperm fossil floras of Skye indicate the climate was cool-temperate to warm-temperate, seasonal and humid. The results from the physiognomic analyses show considerable variation amoungst the climate predictions (Table 6.9). The source of this variation may be the result of methods themselves, which may impose certain biases, but may also be related to factors pertaining to the original source fossil floras of Skye. The following section discusses these potential sources of error to establish a better understanding of how this may influence the climate estimates and the interpretations of the palaeoclimate signal. Four climatic variables are considered here MAT, CMM, WMM and GSP as these variables offer a broader insight into the palaeoclimate and have been predicted by many of the 14 analyses used in this study, and so provide an opportunity for comparison between the methods.

6.4.1 Predictions of MAT

Mean annual temperature estimates derived from the three physiognomic methods show substantial variation between these techniques (Table 6.9, Figure 6.4). Estimates of MAT derived from LMA equations range from -0.1 °C to 8.1 °C, CLAMP 8.6 °C to 12.9 °C and MLR models -2.2 °C to 7.5 °C (Table 6.9, figure 6.4). The LMA and MLR estimates share a similar range although the latter methods estimates are cooler, particularly for MLR2. CLAMP estimates are appreciably higher than those of LMA, 0.4 °C to 13 °C and 1.1 °C to 15.1 °C warmer than the MLR estimates. These results raise important implications regarding the reconstruction of the palaeoclimate signal and the reliability of the physiognomic methods.

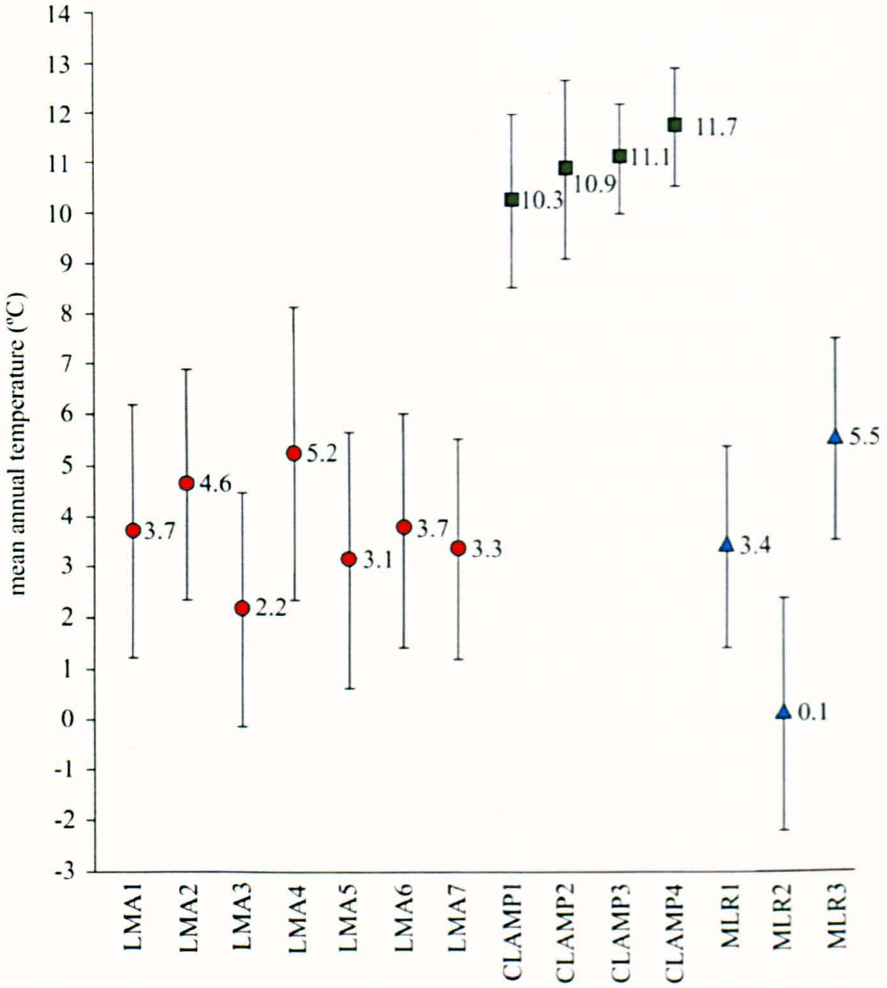

Figure 6.4. Mean annual temperature estimates derived from physiognomic analysis of the mid Paleocene floras of Skye. Red circles ● = estimates derived from LMA transfer functions, green squares ■ = estimates derived from CLAMP analysis, blue triangles ▲ = estimates derived from MLR models.

The correlation of entire margin species and MAT is the primary or sole variable for estimating MAT for the three physiognomic methods (Wolfe 1979, Wolfe 1993, Wilf 1997, Wiemann et al. 1998, Spicer et al. 2005). The discrepancy between the methods is therefore surprising since the margin percentage should be the overriding factor influencing the MAT signal. The addition of physiognomic characters may therefore be the primary cause of this discrepancy. The MAT estimates, however, indicate that addition of physiognomic characters does not necessarily increase precision, as the estimates derived from the MLR models are more consistent with those produced by LMA (Table 6.9, Figure 6.4). Indeed the coldest MAT estimate, 0.1 ± 2.3°C was obtained from MLR2 model, which utilises six physiognomic characters opposed to three for MLR1 and MLR3, which yielded warmer estimates (Table 6.9, Figure 6.4).

A similar discrepancy between LMA and CLAMP derived estimates of MAT was recorded from the early Paleocene floras of Williston and Raton basins of western United States (Davies-Vollum 1997). The appreciably warmer CLAMP estimates were suggested by Davies-Vollum (1997) to be the result of the other physiognomic characters present in the floras that were influencing the MAT estimation. The three primary physiognomic characters that may have influenced the temperature signal were the large proportion of leaf morphotypes with acute bases, a small proportion of small leaves and a small proportion of wide leaves (Davies-Vollum 1997). This physiognomic composition is similar to that of the Skye floras (Table 6.4), and could therefore account for the warmer CLAMP derived estimates.

The MLR models used in this study utilise these traits for their analyses and should therefore be influenced by these character traits in similar way to CLAMP, but as the estimates show, this is not the case. Why CLAMP based MAT methods are providing a warmer MAT signal is currently unclear. The estimates of MAT in this study have to be reviewed in light of other sources of error related to fossil assemblages themselves (see section 6.4.4), other independent climate proxies or indicators from the BTVP and Northern Europe from this interval.

6.4.2 Predictions of seasonality

The seasonality of the palaeoclimate, i.e. how cold or warm the winter and summer temperatures were, has important implications for reconstructing the past climates of Skye. Two climatic variables CMM and WMM have been estimated using the four CLAMP analyses and two of the MLR models (MLR1 and MLR2). The CLAMP derived estimates for CMM are reasonably consistent with a range of -3.0°C to 4.2 °C and for the MLR models are considerably colder and more variable with a maximum range of -18.3 °C to -4 °C. Estimates of WMM, however, are more consistent between CLAMP and MLR models with ranges of 19.0 °C to 24.4 °C and 17.1 °C to 25.8 °C respectively (Table 6.9 and Figure 6.5).

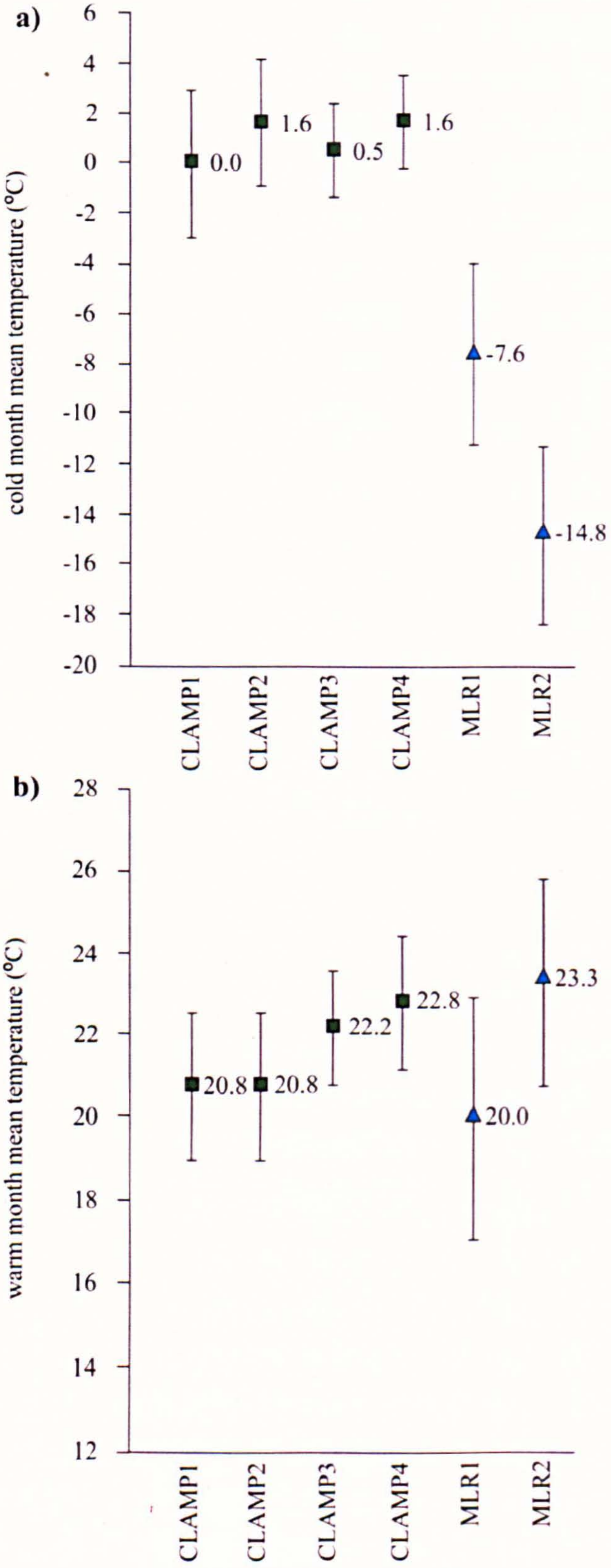

Figure 6.5. a) cold mean month temperature (CMM), b) warm mean month temperature estimates derived from physiognomic analysis of the mid Paleocene floras of Skye. Green squares 🟩 = estimates derived from CLAMP analysis, blue triangles ▲ = estimates derived from MLR models.

Both physiognomic methods indicate that the mid Paleocene winter conditions on Skye were cold with frequent frosts, but the estimates of CMM derived from the MLR models suggest that the winters were severe with hard frosts. The CMM estimates derived from the MLR models appear to be unrealistically cold for such a warm interval as the Paleocene (Zachos et al. 2001) and are considered unreliable.

The cause of the discrepancy between the CMM estimates is unclear. The MLR 1 model is influenced by the presence of emarginate apexes, which if in high relative abundance in a flora predict warmer CMM estimates. However, as Greenwood and Wing (1995) state, leaf types with emarginate apexes are relatively rare components of Eocene floras of North America, and are therefore likely to provide cooler MAT and CMM estimates when using the MLR 1 model. The absence of this character trait on Skye could account for the colder CMM estimates for MLR1.

The estimates of WMM derived from both CLAMP and MLR models have provided similar estimates of the summer temperatures on Skye during the mid Paleocene. These estimates suggest that the temperatures during the summer months were warm, which may facilitated the growth of the plants during these months.

The physiognomic analysis of the floras of Skye suggest that the climate during the mid Paleocene was seasonal with cool to cold winter temperatures and warm summers. These results will be compared in light of other sources of error related to the fossils floras themselves and how comparable they are to other proxies.

6.4.3 Predictions of precipitation

Growing season precipitation (GSP) was selected as an indicator of the past precipitation patterns of Skye as it can be predicted by CLAMP and all three of the MLR models. The estimates derived from both methods are within error of each other and have a range of 1175.6 mm to 2266.7 mm. The gridded climate data derived CLAMP estimates (CLAMP1 and CLAMP3) of precipitation, as discussed in Section 6.3.2, produce drier estimates and so are considered less reliable for this parameter.

The estimates of GSP indicate that the climate of Skye was humid with substantial levels of precipitation during the growth period of the vegetation (Table 6.9, Figure 6.6). The level of precipitation is comparable with that of modern temperate rainforests, which occur in regions with mean annual precipitation (MAP) that exceeds 1400 mm (Alaback 1991). GSP represents the precipitation for months during the growing season, but the estimates obtained from the Skye floras exceed the MAP requirements of this forest type. A single estimate of MAP was determined by MLR1 (Table 6.9) which provided an estimate of 2521 ± 580mm, which indicates these forests received high levels of rainfall.

The seasonality of precipitation patterns has been estimated by the CLAMP analyses and indicates that wetter and drier months precipitation are comparable, excluding gridded derived estimates which are considered unreliable. The three wet month precipitation for CLAMP 2 and CLAMP4 range from 695 mm to 1051 mm and for the three dry months range from 514 mm to 770 mm respectively (Table 6.9). These estimates show there was little seasonal variation in precipitation patterns and the climate was probably annually humid.

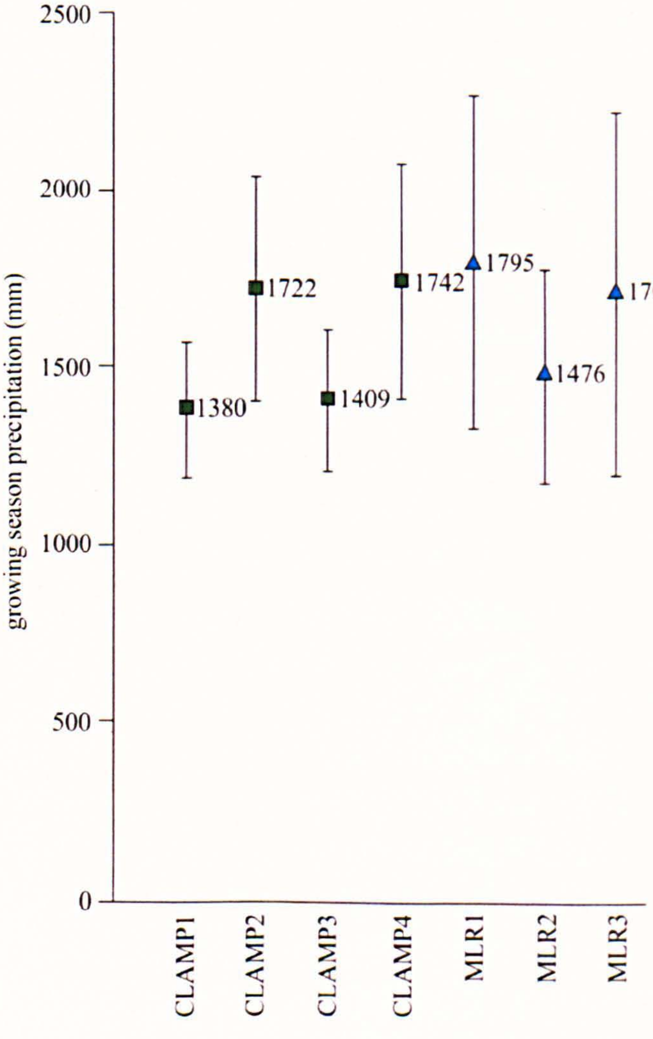

Figure 6.6. Growing season precipitation estimates derived from physiognomic analysis of the mid Paleocene floras of Skye. Green squares ■ = estimates derived from CLAMP analyses, blue triangles ▲ = estimates derived from MLR models.

Precipitation estimates derived from physiognomic methods have been scrutinised for their reliability (Wiemann et al. 1998). In environments where water is not limiting (mesic conditions) leaf physiognomy has proven to be weakly correlated with precipitation, and when CLAMP and MLR models are calculated for modern sites they often over-predict the precipitation of these sites (e.g. Wing and Greenwood 1993, Jacobs and Denio 1996, Wilf et al. 1998). Other physiognomic methods have been developed that rely on average leaf area of specimens (Wilf et al. 1998), but these techniques have not been employed in this study as the leaf specimens from Skye are too fragmentary.

Determining precipitation level precisely for the mid Paleocene of Skye is difficult due to the potential uncertainties of the physiognomic methods, but what can be established is that the climate was humid and precipitation during the growing season was within the limits of modern temperate rainforest (Alaback 1991).

6.4.4 Other potential sources of error

6.4.4.1 Low floral diversity

Low diversity of woody dicots in fossil assemblages has been regarded as a major source of potential error for estimation of palaeoclimates (Burnham 1989, Wolfe 1993, Wilf 1997, Burnham et al. 2001, 2005). Low floral diversity (small number of morphotypes) is potentially a significant problem for univariate methods such as LMA if the ratio of the entire margined or toothed species is skewed. If the margin percentage for a flora is around 50% then floral diversity has to be high within an assemblage to ensure that this value is statistically significant (Wilf 1997).

Woody dicot diversity in the Skye flora is relatively low with 14 morphotypes recognised, and only 12 with margin preserved. The floras of Skye are dominated by toothed morphotypes (Table 6.2) and hence have provided estimates of cool climates. The low diversity could potential mask the true ambient climate conditions, but because the flora is so heavily skewed to toothed taxa (91.7%) it is unlikely that this composition is the result of limited diversity. Indeed, for such a skewed margin percentage the necessity for high floral diversity diminishes (Wilf 1997). The calculated sampling error for LMA according to Wilf (1997) for the Skye floras shows that error is relatively low at 2.2 °C to 2.9 °C (Table 6.3). The sample error for the LMA equations is near to the minimum suggested by Wilf (1997) for MAT predictions from physiognomic methods and suggests that the low diversity of the Skye floras has not adversely affected the accuracy of the MAT predictions.

Limited floral diversity is also a concern for multivariate methods such as CLAMP analysis for which a minimum of 20 species/morphotypes is recommended for the analysis (Wolfe 1993).

Higher floral diversity is likely to capture the fuller range of physiognomy and reduce the effect of extreme or anomalous morphologies. In this study 15 morphotypes were used in the CLAMP analysis, which is below that recommended by Wolfe (1993). The physiognomic composition is distinctive and displays a narrow range of character states (Table 6.4). The flora is dominated by unlobed, toothed, large leaves, with acute or attenuate apexes, all base shapes, shorter L:W ratios and elliptic leaves. The physiognomic composition shows that there is relatively little physiognomic variation between morphotypes and perhaps the limited diversity has had little impact on the climate signal because the physiognomy is consistent.

The effects of low diversity in this study cannot be directly solved and this is an issue for many Paleocene floras which often have reported low woody dicot diversity (e.g. Hickey 1980, Davies-Vollum 1997, Gemmil and Johnson 1997, Peppe 2010). The palynological record of Skye also confirms the relatively low angiosperm diversity of this region (Jolley 1997). The leaf assemblage of Allt Mor contains a high proportion of the angiosperm types represented in the pollen record, which indicates that the relatively limited diversity of angiosperms is a true ecological signal and not the result of limited preservation.

6.4.4.2 Taphonomy and preservation

The impacts sorting and depositional environments have on the preservation of leaf assemblages has been discussed in Chapter 5 (see section 5.3.2.3), but the impacts these factors have on palaeoclimate predictions can be significant. The loss of foliar characters due to transport, decomposition and preservation has been shown to have a profound impact on the climate estimates (Greenwood 1992, Spicer et al. 2005).

In the Skye flora leaf preservation, as discussed in Chapter 3 (see section 3.5), is variable and is overall relatively poor for the majority of the leaf specimens. The leaf assemblage at Allt Mor is dominated by small fragmented leaves (96%), which provide limited physiognomic information. The limited preservation of the floras is to certain extent mitigated by the presence of leaf specimens for each morphotype that are well preserved, and have a high proportion of physiognomic traits present. Traits such as margin, lamina size, base shape and lamina shape are well represented by the leaf specimens (Table 6.10). The completeness of each of morphotype i.e. the total number of characters present to be scored for each of the character categories is variable, ranging from 100% to 43% (Table 6.10). The overall completeness of the flora is 60%, which is the minimum suggested by Spicer et al. (2005) for CLAMP. Although the Skye floras are at the lower end of completeness the climate signal they provide should be reliable.

Table 6.10. Physiognomic character preservation of the angiosperm morphotypes of Skye.

Morphotype	Dissection	Margin	Size	Apex	Base	L:W	Shape	Completeness (%)
AM1 *Platanites hebridicus*	-	X	X	-	X	X	X	86
AM2 *Trochodendroides antiqua*	X	X	X	X	X	X	X	100
AM3 *Corylites hebridicus*	X	X	X	X	X	X	X	100
AM4 "*Corylites* cf."	X	X	X	X	X	X	X	100
AM5 *Fagiosiphyllum groenlandica*	X	X	X	-	X	-	-	57
AM6 *Juglandiphyllites* sp.1	X	-	X	-	X	-	X	57
AM7 *Juglandiphyllites* sp.2	X	X	X	-	X	-	X	71
AM8 "*Platycarya* cf."	X	X	X	X	X	X	X	100
AM9 *Vitiphyllum sewardii*	X	X	X	X	X	X	X	100
AM10 *Cornophyllum hebridicum*	X	X	X	X	X	X	X	100
AM11 *Zizyphoides* sp.	X	X	X	X	X	X	X	100
AM12	X	X	X	-	-	-	-	43
AM13	X	X	X	-	X	-	X	83
AM14	X	-	X	-	X	-	-	43

AM= angiosperm morphotype, L:W= length:width ratio, X= presence of scorable characters, - = absence of character trait, dissection = presence of lobing.

Depositional environments may artificially alter the composition of a fossil floral assemblage through selective sorting or preservation (Roth and Dilcher 1978, Spicer 1981, Scheihing and Pfefferkorn 1984, Ferguson 1985, Burnham 1989, Spicer 1989, Greenwood 1992, Behrensmeyer et al. 1992, Burnham et al. 1992, Gastaldo et al. 1995). The leaf assemblages of Skye, as discussed in Chapter 5 (see section 5.3.3.2), were deposited in a pond environment close to fluvial system. The composition of the flora suggests that it contains elements of the local and more regional environment and therefore should provide not just a local but more regional climate signal.

Environments with waterlogged or wet soils have been shown to have a higher relative abundance of woody dicots with toothed margins compared to coeval stands in drier sites (Burnham et al. 1992, Kowalski and Dilcher 2003). This phenomenon is thought to be caused by the need of plants growing in wet environments to rapidly transpire water from the leaves to facilitate root function in waterlogged environments (Burnham et al. 1992, Kowalski and Dilcher 2003, Royer et al. 2009). Fossil plant assemblages are often associated with saturated soil environments such as riparian, lacustrine and swamp conditions (Roth and Dilcher 1978, Ferguson 1985, Spicer 1989) and so may provide cooler climate estimates.

The leaf assemblages of Skye were deposited in fluvial settings and are associated with floodplain and swampy conditions where soil saturation may have been high. It is possible therefore that the floras may have an enriched toothed component, which could lead to cooler climate estimates. Kowalski and Dilcher (2003) produced an LMA transfer function to take into account the effects that wet soils may have had on MAT estimates.This transfer function, although still in an experimental stage, provided more accurate MAT estimates for wet soil sites in Florida. This transfer function was applied to the floras of Skye (LMA4), and produced the warmest MAT estimate (5.2 ± 2.9°C) derived from any of the LMA transfer functions. This estimate suggests the MAT signal derived from the floras of Skye may be cooler due to the effect of wet soils. But the estimates obtained from LMA4, although warmer are still within error of the LMA derived estimates, which suggests that if there was an effect due to wet soils, it was minimal.

6.4.4.3 Altitude

The relative elevation of the leaf assemblages of Skye may have a strong influence on the climate estimates obtained in this study. If the floras represent upland sites at higher elevations then the climate signals obtained may indicate a cooler climate than coeval floras at lower elevations or at sea level.

Jolley (1997) suggested that the topography of the Skye Lava Formation was dynamic with significant uplift and subsidence events. The Allt Mor plant assemblage was suggested by Jolley (1997) as being an upland site, with an elevation of approximately 1000 m. This interpretation was based on the thickness of the overlying Cruachan Lava Formation and the upland-aspect of the palynomorph assemblage. As stated in Chapter 5 (see section 5.4.2.2) the palynomorphs of Allt Mor are poorly preserved and low in abundance. The leaf fossils are more indicative of the Allt Mor Carbostbeg locality, which was interpreted by Jolley (1997) as a lowland site.

The uplift events were suggested by Jolley (1997) as being caused by inflation due to magma generation and the uplift of Cullins. The first factor may have certainly have caused a rise in topography but to what extent is difficult to ascertain. The second factor the, development of

Cullins is not supported by field observations (Williamson and Bell 1994) or radiometric dating (Hamilton et al. 1998), which both show that the Cullins are younger than the Skye Lava Formation. Based on this evidence there is little to suggest that the floras of Skye were at elevations as great as 1000m.

The sediments of the Minginish Conglomerate Formation indicate that the early development of this formation was characterised by fast flowing streams and mass movement deposits. As the depositional environment matured floodplains and swamps developed (Williamson and Bell 1994). These environments are more indicative of lower topographical gradients and not mountainous conditions. The sediments of the Minginish conglomerate seem to suggest that the floras of Allt Mor developed in a more lowland setting that permitted the development of floodplains and swamps. Altitude may have had some influence on the palaeoclimate estimates but these effects appear to be slight, and the cool climate signal derived from the Skye flora indicates that climate was indeed cool.

6.5 Palaeoclimate of Skye

The palaeoclimate estimates derived from the leaf physiognomy of the Skye floras has provided evidence of the climatic conditions in this region during the mid Paleocene. Estimates of MAT indicate that the climate was cool-temperate to temperate (-0.1 °C 12.9 °C), with significant seasonal variation. Winter conditions were cool to cold (-18.3 °C to 4.2 °C) and frosts may have been frequent, while in the summer, temperatures were warm (19.0 °C to 25.8 °C) and would have provided favourable growing conditions for the vegetation. Precipitation estimates indicate that the climate was humid with high levels of precipitation falling in the growing season (1175.6 mm to 2266.7 mm). The three methods used in this study (LMA, MLR and CLAMP) have produced conflicted climatic evidence highlighting the importance of using multiple physiognomic techniques and other proxies to decipher palaeoclimates.

Because of these potentially conflicting climate estimates, climate indicators and proxies from the mid Paleocene of Skye, the BTVP and Northern Europe will be considered. These other lines of evidence will firstly test the validity of the results in this study, and secondly will help determine which physiognomic method has provided the most accurate palaeoclimate estimates.

6.5.1 Floral climate indicators

The fossil floras of the BTVP have been studied extensively for well over a century and have provided a wealth of information on the taxonomic composition, vegetation structure and palaeoecology of these floras. Both quantitative and qualitative assessments based on the fossil floras of the BTVP have led to varying climatic interpretations. Some researchers (e.g. Seward and Holttum 1924) suggested that the climate was temperate due to the high abundance of deciduous plant types present in the plant beds of Ardtun on Mull. While other researchers (Boulter and Kvacek 1989, Jolley 1997) have argued that the composition of the BTVP floras is more indicative of warm temperate to subtropical climates.

The composition of the leaf and palynomorph assemblages of Skye are not considered here as indicative of subtropical climates. The absence of thermophillic taxa such as palms, oaks, laurels or magnolia is more suggestive of temperate conditions. The study by Wolfe (1979) has provided an important framework for the vegetation patterns and their climate tolerances from the floras of East Asia. In Wolfe (1997) two important floral indicators of climate that are significance for this study were noted from the floras of East Asia. Firstly, woody dicots that produce notophyllous evergreen leaves only occur in regions where the CMM is greater than 1 °C. Secondly, deciduous woody dicots become increasingly more diverse and abundant in regions where MAT is 10 °C or lower. The absence of notophyllous evergreen vegetation and the dominance of deciduous broadleaved taxa in the Skye floras indicates that the estimates of MAT (-0.1 °C to 12.9 °C) and CMM (-18.3 °C to 4.2 °C) obtained in this study are reliably reflecting the vegetation composition.

Fossilised wood recovered from the BTVP and deposits from the Paleocene-Eocene London Clay have provided climatic signals from these two regions. The wood fossils from the London Clay typically lack distinct growth rings and have a high vulnerability index, this morphology was suggested by Crawley (1989) as an indicator of equable subtropical climatic conditions. Wood from the BTVP, however, possesses well developed rings and has a low vulnerability index. The wood from the BTVP is more indicative of cooler, seasonal climatic conditions with periods of water stress, possibly induced by freezing conditions (Crawley 1989, Woolnough and Overnell 2006). The wood record is in close agreement with that of physiognomic estimates for the BTVP, as both indicate cooler seasonal climates with possible winter frosts.

The fossil floras of Ardtun Mull, are exceptionally well preserved and share many of the plant taxa found in the Skye leaf assemblages. The climate of Ardtun has been suggested to have been warm-temperate to subtropical (e.g. Boulter and Kvacek 1989, Jolley 1997). The climatic interpretation of this flora is not discussed further in this section but is presented in Chapter 7 (see section 7.5), where the physiognomic analysis of this flora has been applied.

Paleocene floras from Western Europe have been identified in southern England, France, Belgium and Germany. These floras contain floral elements that are shared between both Skye and Europe. These include members of the families Platanaceae, Cercidiphyllaceae, Betulaceae, Juglandaceae and Cupressaceae, which suggests that some degree of floral connectivity existed between Scotland and Europe during the Paleocene (Crane 1981, Crane and Manchester 1982, Crane 1984, Mai 1995, Collinson and Hooker 2003, Kvacek 2010). The fossil floras of western

Europe do, however, differ considerably to those of Skye, despite of these shared taxa. The floras of western Europe are more typical of subtropical or paratropical climates and contain a large proportion of thermophilic taxa, particularly members of the Lauraceae and Fagaceae (Mai 1995, Collinson and Hooker 2003, Kvacek 2010).

The physiognomy of Western European floras is significantly different to that of Skye, as a high proportion of the leaf types are notophyllous evergreen (Mai 1995). This indicates that the climate of western Europe during the Paleocene was subtropical to paratropical with mean annual temperatures greater than 13 °C but less than 25 °C, with mild winters with cold mean month temperatures above 0 °C (Wolfe 1987, Mai 1995, Collinson and Hooker 2003, Kvacek 2010).

6.5.2 Sedimentary climate indicators from the BTVP

The sedimentary sequences of the BTVP have provided a wealth of information on the sedimentary processes, deposition patterns and palaeoenvironments of this region during the mid Paleocene. The presence of climate-sensitive sediments and features such as coals, laterites and mass movement/wasting deposits may provide indications of the palaeoclimate.

Coals have been used as indicators of palaeoprecipitation patterns as they form in restricted conditions where rainfall, anoxia and plant productivity are high (Parrish et al. 1982). The distribution of Late Cretaceous and Paleogene coals indicates they formed in tropical low latitudes and cooler mid-high latitudes, a pattern which is consistent with modern peat accumulation patterns (Parrish et al. 1982). Lignite deposits are found across the BTVP, including the plant-bearing sections of the Minginish Conglomerate Formation (Williamson and Bell 1994, Brown et al. 2009). The presence of lignites on Skye and elsewhere in the BTVP is a strong indicator of high levels of precipitation. It is difficult to ascertain temperature from the coals, although these lignite deposits may represent temperate peat accumulation or conifer dominated swamps.

Mass movement and mass wasting deposits occur throughout the BTVP and have been attributed to a wide variety of processes, ranging from small scale alluvial fans to caldera collapse (Brown et al. 2009). These mass movement events were facilitated by the tectonically active setting of the BTVP and the ambient climate conditions, which were suggested by Brown et al. (2009) to have been warm and humid.

The rapid unroofing of the Rum central volcano indicates that weathering and erosion was intense in the BTVP. The Rum central volcano and Canna Lava Formation were generated and subsequently eroded within an interval of ~0.92 million years (Emeleus 1983, Pringle and Parrish 2005, Brown et al. 2009). The erosion rates have been estimated to have been 1.8mm per year, which is comparable with that of the Himalayas (Pringle and Parrish 2005, Brown et al. 2009). Brown et al. (2009) suggest that the rapid uplift caused by the development of the central volcanoes of the BTVP and the warm wet climate provided optimum conditions for rapid erosion.

The Eynort Mudstone Formation of west-central Skye is another indicator of humid climatic conditions as the sediments of this formation have been interpreted as being deposited in ephemeral lakes which were fed by the products of weathering from the surrounding lava field (Williamson and Bell 1994). Laterite sequences occur in the Eynort Mudstone Formation and indicate periods of emergence, development of palaeosols and intense chemical weathering (Williamson and Bell 1994). The presence of laterites is also a strong palaeoclimate indicator. Modern laterite development is restricted to regions with warm humid climates such as the tropics and subtropics (Scotese and Golonka 1992). The distribution of laterites has been used as palaeoclimate indicator due to the specific climate-related development patterns (Scotese and Golonka 1992).

The dependence of warm, wet tropical climatic conditions for laterite development has been questioned due to the presence of laterites in high latitude Cenozoic sites in Australia, Iceland and Northern Ireland (Nilsen 1978, Taylor et al. 1992, Hill et al. 2000, Tabor and Yapp 2005). Basalt sequences in the Monaro Province of New South Wales, Australia contain interbasaltic laterites that span from the late Paleocene into the Oligocene (Taylor et al. 1992). The Paleocene laterites in the Monaro Province formed at a relatively high palaeolatitude of ~57.5°S (Taylor et al. 1992). The climate of this region has been interpreted as cool-temperate rainforest (comparable to Tasmania and southern New Zealand) based on palaeobotanical and oxygen isotope evidence (Idnurm 1985, Bird et al. 1990, Taylor et al. 1990, Taylor et al. 1992).

The formation of laterites under this climate regime suggests they were capable of forming in non-tropical conditions. Taylor et al (1992) suggest that warmer summer temperatures, low erosion rates and high precipitation facilitated the slow development of laterites in this cool climate. The study by Taylor et al. (1992) has been questioned by Retallack (2008) who suggested that the lateritic bauxites of the Monaro Province developed during episodes of acute climate warming in the late Paleocene and Eocene.

Extensive laterite deposits are present within the Interbasaltic Formation of the Antrim Lava Group, Northern Ireland (Williamson and Bell 1994, Hill et al. 2000). The laterite sequences of the Interbasaltic Formation are extensive and measure up to 30 m (Hill et al. 2000). The development of such thick laterite sequences indicates that there was a prolonged hiatus in volcanic activity and intense weathering. These laterites contain a high abundance of gibbsite, which was interpreted by Hill et al. (2000) as an indicator of heavy rainfall, good drainage, and high temperatures in subtropical climates. Atmospheric CO_2 concentrations have been determined form these laterite sequences, which indicate that atmospheric CO_2 was ~2400 ppmV during this interval (Tabor and Yapp 2005).

Dating of the Interbasaltic Formation and the underlying and overlying Lower and Upper Basaltic formations of Antrim indicate that these sequences are older than Hebridean elements of the BTVP (see Chapter 2, section 2.3). The Tardee Rhyolite, an intrusive feature within the Interbasaltic Formation, has been dated as 61.3 ± 0.3 (Ganerød et al. 2010), and the Skye floras have been dated as 60.28 ± 0.45 Ma (Hamilton et al. 1998, Chambers and Pringle 2001). The laterites of the Interbasaltic Formation may have therefore formed in warmer interval in the Paleocene, which facilitated the development of the laterites.

The absence of such extensive laterites on Skye and elsewhere in the BTVP may support this assertion that the conditions for laterite development became less favourable through the course of the mid Paleocene. The laterites that do occur within the Skye Lava Formation are often thin (Williamson and Bell 1994) and in some instances they may represent weathered tuffs, rather than true laterites (Bell et al. 1996, Emeleus et al. 1996). The warm summer temperatures and high precipitation estimates from the floras of Skye indicate that conditions may have been suitable for limited laterisation in a cool climate state indicated by Taylor et al. (1992). Detailed study of the laterite deposits of the BTVP is required to firstly ascertain if they are true laterites, and to what climate conditions they may have formed in.

6.5.3 Mid Paleocene marine climate record of Europe

Oxygen isotope records from the North Sea have yielded temperature estimates that indicate cool sea temperatures and gradual warming in the late mid-Paleocene. Stable oxygen isotope ratios from mollusc shells indicate that sea surface temperatures (SST) at ~60 Ma were cool and range from 10 °C to 14 °C (Buchardt 1977, Buchart 1978). Sea surface temperatures in the North Sea show a gradual increase to 11 °C to 16.5 °C at ~58 Ma (Buchardt 1977, Buchart 1978).

The SST estimates were, however, derived from bulk shell sampling, and the bivalves used were assumed to have dwelled in soft bottom communities at depths of 30 m to 150 m with no thermocline (Buchardt 1978).The results of this study are possibly unreliable, due to its methodology and the assumptions made. A more recent study using intrashell aragonite of Danish bivalves has suggested much warmer sea surface temperatures during the mid Paleocene. Summer SST estimates for the Danish North Sea were between 22-28 °C, and winter SST >13 °C (Schmitz 2003).

Iberian reefs show significant changes at the Danian-Selandian (61.7 ± 0.2 Ma) transition (Baceta et al. 2005, Aguirre et al. 2007). A hiatus in reef record extends across much of the Selandian, which is related to falling sea levels (Baceta et al. 2005, Aguirre et al. 2007). The reefs that are preserved from the late Selandian into the Thanetian (~59 to 58 Ma) are less diverse, and the main reef constructors are dominated by calcareous algae (Baceta et al. 2005). Calcareous algae diversity remained fairly constant throughout the Danian and suddenly increased from 11 to 29 species in the Selandian (Aguirre et al. 2007). This diversity decline and ecological shift is suggested by Baceta et al. (2005) to have been caused by climate cooling, rather than decline in nutrients or an increase in siliclastic sediment input. The composition of the calcareous algae also shows marked changes at the Danian-Selandian boundary. The tropical sporolithaceans become replaced by the melobesioids algae which are tolerant of broader range of temperatures, indicating cooler marine conditions in this region (Aguirre et al. 2007).

Similar compositional shifts have been observed in foraminifera from the North Atlantic, which show a marked shift from thermophillic to cool water Arctic taxa between 60 to 58 Ma (Haq et al. 1977). The southward shift of cool water taxa into the Atlantic was suggested by Haq et al. (1977) as representing cooling during this interval, but oxygen isotope records from their study did not detect the decline in marine temperatures.

6.6 Summary

The fossil angiosperm leaves of Skye have provided the first quantitative estimates of palaeoclimate for this region. Three physiognomic methods have been utilised in this study and include LMA, CLAMP and MLR models. In total 14, separate analyses have been used to determine the palaeoclimate.

The estimates obtained from the Skye floras have provided a mixed picture of the palaeoclimate. Climate estimates derived from LMA and MLR models indicate that the climate was cool-temperate to temperate with a MAT of -0.1 °C to 8.1 °C and -2.2 °C to 7.5 °C respectively. MAT estimates obtained from CLAMP are appreciably warmer with a range of 8.6 °C to 12.9 °C. The seasonality of the climate during the mid Paleocene has been estimated based on results of CMM and WMM. These parameters indicate the winters were cool and frosts may have been common, and possibly severe, while the summers were warm. Estimates of precipitation indicate that the climate state was humid and comparable with modern temperate rainforest conditions (MAP >2000 mm). The variability of the climate estimates highlights the possible problems of using a single physiognomic method to decipher climate signals from leaf physiognomy.

Factors that may have resulted in inaccurate climate signals have been recognised and include low floral diversity, preservation, taphonomy, wet soils and altitude. These factors may have led to cooler temperature estimates and therefore the upper range of the LMA and MLR estimates of the MAT are considered more reliable.

Independent climatic indictors from the BTVP and Northern Europe have provided a mixed picture of the mid Paleocene climate. The climate of western Britain during the mid Paleocene appears to have been humid, with high levels of precipitation indicated by leaf physiognomy and sediments of the BTVP. The floras of Skye indicate that the climate was cool temperate but the presence of extensive laterite sequences in the Interbasaltic Formation of Antrim, Northern Ireland are more indicative of warm subtropical conditions. The laterite deposits of the BTVP are, however, only extensive in Antrim and, the radiometric dating of these sequences suggests these deposits are 0.5 m.y to 1 m.y older than the floras of Skye. The laterite deposits may have therefore formed under more favourable conditions earlier in the Paleocene.

Oxygen isotope records from bivalves of the North Sea indicate cool sea surface temperatures comparable with flora record (Buchart 1977, 1978). Although more recent research suggests warm summers and mild winter conditions in the Danish North Sea (Schmitz 2003). Reef building calcareous algae and foraminifera from Western Europe and the Atlantic suggest that the climate became cooler during the mid Paleocene 60 to 58 Ma (Haq et al. 1977, Baceta et al. 2005, Aguirre et al. 2007), which supports cool temperature estimates derived from the floras of Skye.

The MAT estimates derived from LMA and MLR models may have under predicted the temperature, while CLAMP may have overestimated this parameter. The overlap between these estimates at 5 °C to 9 °C may be a more accurate estimation of the actual MAT, as this range encompasses the majority of the physiognomic estimates and is more comparable with the independent climate indictors.

Chapter 7: Paleocene environments, floras and climate of Mull

7.1 Introduction

The Paleocene fossil floras of the Ardtun leaf beds on the Isle of Mull are well known and have been extensively studied for over a century (Forbes 1851, Bailey 1869, Gardner 1887, Gardner and Ettinghausen 1879-1882, Gardner 1883-1886, Seward and Holttum 1924, Johnson 1914, 1933, 1937, Johnson and Gillmore 1921, Crane 1984, Crane 1988, Crane et al. 1988, Boulter and Kvacek 1989). The exposures on Mull have been extensively excavated and now it is difficult to collect new specimens from the leaf-bearing strata. Good collections of the plant macrofossils are present at the Natural History Museum, London; British Geological Survey at Keyworth, Nottinghamshire; National Museums of Scotland, Edinburgh; and the Hunterian Museum, Glasgow. The extensive collections can provide sufficient information so new collections from Ardtun were not required for the purposes of this study. To date publications on the Mull flora have concentrated on the taxonomic identity of the flora, morphological descriptions and their biogeographic significance. Only Royer et al. (2001) have used the *Ginkgo* leaves to determine atmospheric CO_2 levels from this flora. A detailed analysis of the leaves for palaeoclimate estimates has not previously been undertaken.

This chapter includes information on the geological setting of the Mull flora, its age, summary of the floral composition based on published reports of the taxa, and new observations undertaken for this study of the collections from the Natural History Museum, the Geological Survey and the National Museums of Scotland. The woody dicot leaves were scored for palaeoclimate analysis according to the same methodology as outlined in Chapter 6.

7.2 Geological setting of the Mull flora

7.2.1 Mull Lava Group

The Mull Lava Group (MLG) covers most of the Isle of Mull, and extends north and west into the Inner Hebrides Trough and onto the mainland in Movern and eastern Ardnamurchan (Kerr 1995) (Figure 7.1). The lava fields of Mull are the thickest within the British Tertiary Volcanic Province (BTVP) and measure up to ~1000 m, although the original thickness would have been much greater (Kerr 1995). The Mull Lava Group is subdivided into the Staffa Lava Formation, overlain by the Mull Plateau Lava Formation (Kerr 1995). The lavas of the Staffa Lava Formation are ~25 m thick and lie unconformably on Cretaceous carbonate sediments and Middle Jurassic clastic marine units (Kerr 1995). The lavas of the Staffa Lava Formation show columnar-jointing, pillow structures and are associated with hyaloclastite facies (Keer 1995). These features along, with the sedimentary sequences between the lavas of the Staffa

Formation, indicate that the lavas formed in a subaqueous setting associated with lacustrine or swamp conditions (Kerr 1995).

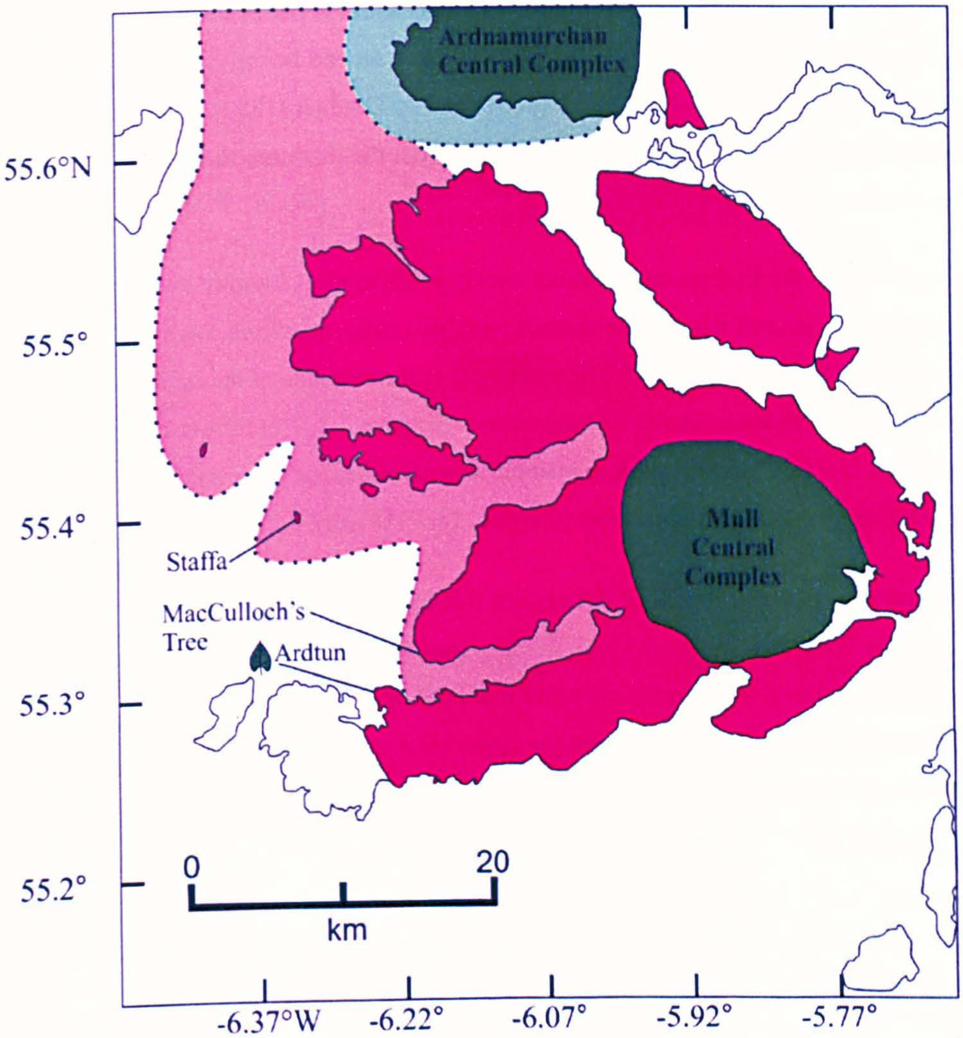

Figure 7.1. Map of the Isle of Mull showing the extent of the onshore and offshore sequences of the Mull Lava Formation, and the Mull and Ardnumurchan central complexes. The location of the Ardtun leaf beds (denoted by leaf) and the Maculloch's Tree locality used for radiometric dating (Chambers and Pringle 2001) are shown.

The Staffa Lava Formation is overlain by the much more extensive Plateau Lava Formation which is subdivided into the Ben More Main Member and Ben More Pale Member (Kerr 1995) (see Chapter 2, Figure 2.2). Both of these members are largely comprised of interleaved massive basaltic flows. Weathered flow tops are frequent but clastic sediments are currently unrecorded (Kerr 1995, Emeleus and Bell 2005). The presence of weathered flow tops indicates that breaks in volcanic activity occurred, but the lack of clastic sedimentation suggests that these intervals were relatively short.

7.2.1 Stratigraphy and sedimentology of the Ardtun leaf beds of Mull

The lava sequences of the Staffa Lava Formation contain the plant beds of the Ardtun Conglomerate Formation. The sediments of the Ardtun Conglomerate Formation have provided leaf macrofossils, which are reviewed in this study. Three exposures of the Ardtun leaf beds are present in southwest Mull at Ardtun Head (Figure 7.1), two within a ravine in Ardtun (Figures 7.2, 7.3), and the third exposure ~30 m west of other two in a second ravine (Figure 7.4). The Ardtun plant beds have been studied by Argyll (1851) and by Gardner (1887). The description of the sediments and occurrence of the leaves is derived from the literature as no field campaigns were made to Ardtun in this study.

The Ardtun leaf beds at the first ravine exposure overly a ~24 m thick basaltic lava flow, which exhibits columnar joining until it nears the contact with the sediments above, where it becomes amorphous (Argyll 1851, Gardner 1887). The sediments at the east side of the ravine are composed of gravels, sandstones, shales and mudstones (Figures 7.2, 7.3). The dark grey-black shales of the 'black leaf bed' and the dark mudstone above this bed are the only fossiliferous deposits in the eastern exposure of the ravine (Gardner 1887) (Figure 7.2).

The western exposure is similar to that of the eastern side but has been quarried to extract the plant fossils (Figure 7.3). The 'black leaf bed' in this exposure has provided a rich variety of fern, conifer and angiosperm leaf fossils and other plant debris. Another plant bearing bed was exposed by quarrying and this occurs between the upper most gravel and the overlying basalt (Argyll 1851) but was found to be unfossiliferous by Gardner (1887).

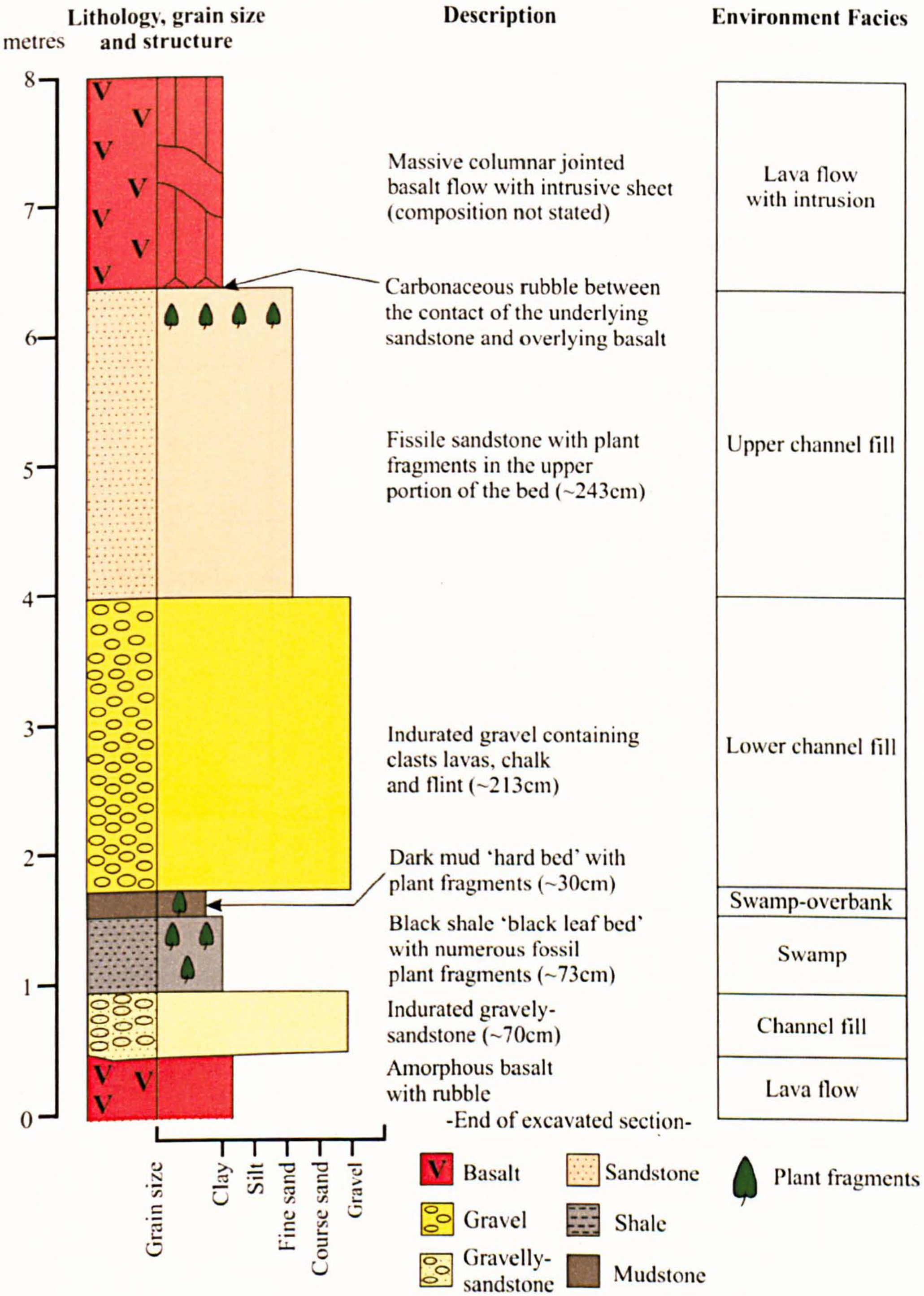

Figure 7.2. Stratigraphic log of the Ardtun Conglomerate Formation exposed on the east side of the first ravine section (NG 13 72) at Ardtun Head Mull. Section based on measurements and field observation from Gardner (1887).

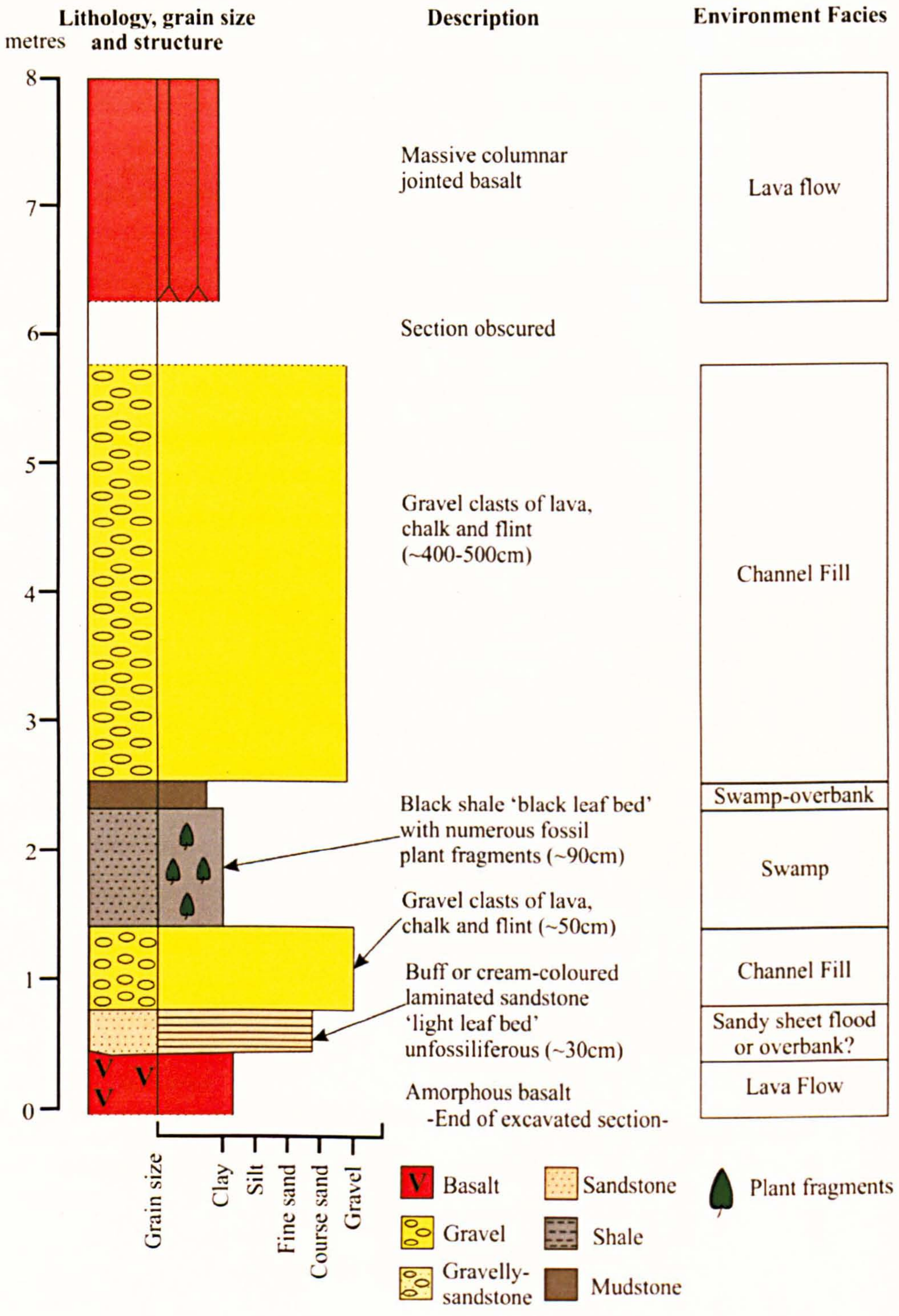

Figure 7.3. Stratigraphic log of the Ardtun Conglomerate Formation exposed on the west side of the ravine section (NG 13 72) at Ardtun Head Mull. Section based on measurements and field observations Gardner (1887).

The exposure in the second ravine shows similar facies patterns to the first ravine sections but has a greater vertical exposure. The second ravine exposure has beds that are present that occur below the basal-most beds of the first ravine exposure, and in addition, has provided some of the best preserved fossil leaves (Gardner 1887, Boulter and Kvacek 1989). The sediments of the second ravine are composed of gravels, sandstones, siltstones, shales, mudstones and fine grained limestones (Figure 7.4). Fossil leaves occur in abundance in the finer grained deposits, but are absent from the gravels (Figure 7.4).

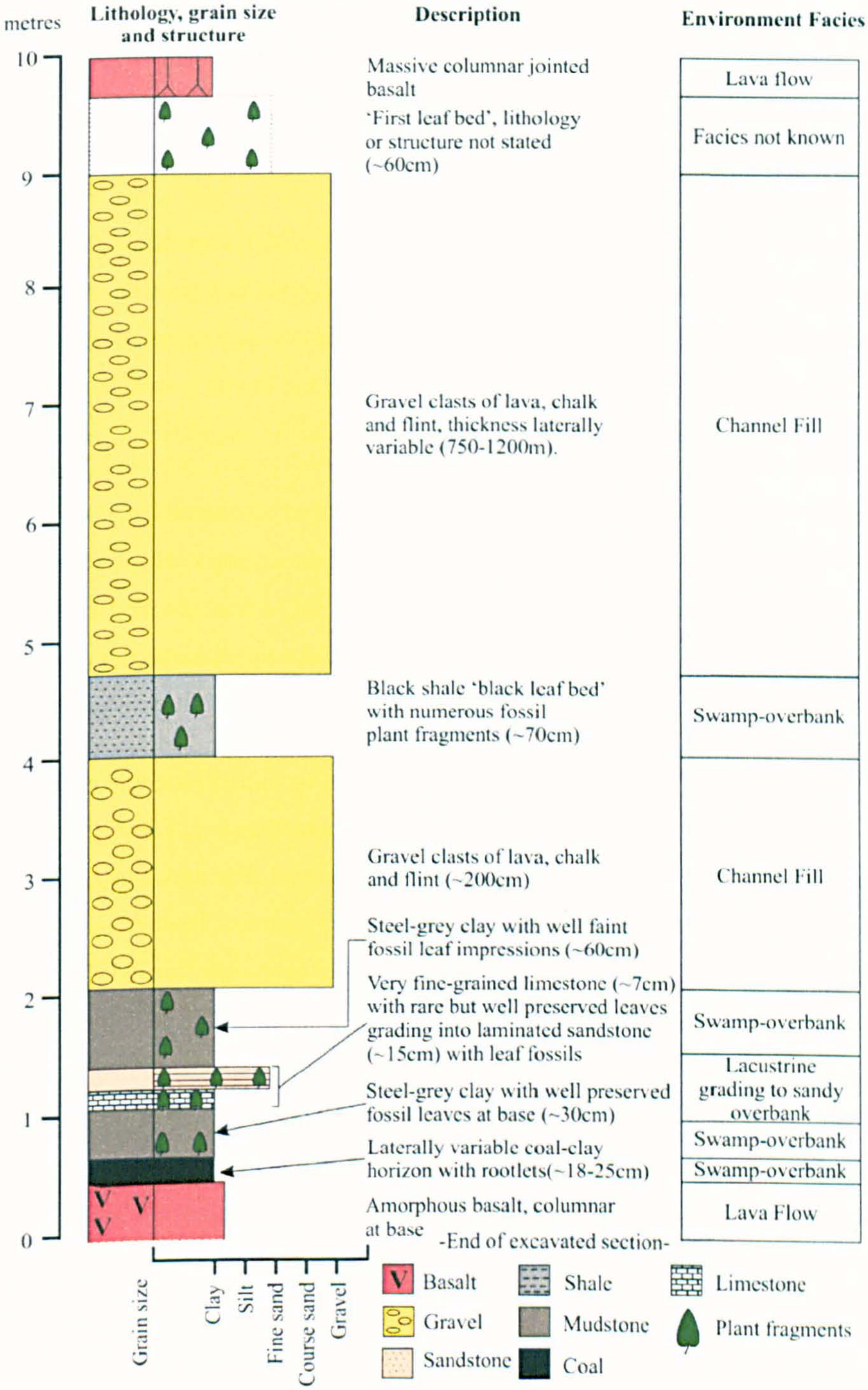

Figure 7.4. Stratigraphic log of the Ardtun Conglomerate Formation exposed at the second ravine section (NG 13 72) at Ardtun Head Mull. Section based on measurements and field observations from Gardner (1887).

The sedimentary sequences of the Ardtun Conglomerate Formation represent depositional environments attributed to fluvial, lacustrine, overbank and swamp conditions. The gravel deposits contain basaltic clasts derived from the local lavas, as well as Cretaceous flints (Gardner 1887, Keer 1995). These gravels probably represent within-channel fluvial deposits, where both basalts and the older Mesozoic marine sediments were eroded, transported and later deposited by the river systems. The clays, shales and limestones are interpreted as overbank and lacustrine facies that developed in association with the river systems. The "black leaf bed" is more characteristic of localised swamp development, as it possesses an organic-rich matrix and an abundance of plant remains.

The depositional pattern at Ardtun Head is similar to that of Minginish Conglomerate Formation of Skye, but the lateral flooding events appear to be of lower energy as fine grained overbank deposits are more frequent. The low frequency of sandstone units that may represent crevasse splay, sheet flood or intense overbank flooding may indicate that the fluvial system was lower course and more meandering compared to the rivers of the Minginish Conglomerate Formation.

Recent investigations of the sedimentary sequences of the Staffa Lava Formation and the palynomorphs they contain have provided new insight into the depositional history of these sediments. Jolley et al. (2009) have interpreted the sediments of the Ardtun Conglomerate Formation as being deposited by an alluvial fan with south-east flowing channels with the finer grained sediments representing channel fill deposits.

The preservation of the leaves is variable at Ardtun Head, the best preserved specimens being restricted to fine grained shales, clays and limestones. Although the "black leaf bed" is a fine-grained shale the leaves within it are not exceptionally well preserved. The dark matrix reduces the clarity of the visible leaf venation, and often the leaves are fragmented. Boulter and Kvacek (1989) also noted that the collection of these specimens may have been selective, with preferential collection of well preserved or particularly complete specimens. The collections from Mull housed at the National Museums of Scotland, Edinburgh, The Natural History Museum, London and the British Geological Survey, Keyworth lack any information pertaining to their original stratigraphical occurrence. These factors therefore make it difficult to determine the ecological relationships between the floras and the palaeoenvironment.

7.3 Dating of the Ardtun leaf beds

The age of the lava sequences, sedimentary horizons and the floras they contain is controversial, with results of radiometric dating at odds with the palynological record. Accurate dating of the Mull floras is essential to understand how this flora fits within the biological and climatic context of the Paleocene.

Reliable radiometric dating of the Staffa Formation near to the exposure of McCulloch's tree (NG 580 468) have provided an age of 60.6 ± 0.3 Ma (Chambers and Pringle 2001). This age is consistent with older published dates for the Staffa Lava Formation of 60.5 ± 0.5 Ma (Mussett 1986). The sample at the McCulloch's tree exposure is stratigraphically comparable with the Ardtun Conglomerate Formation (Kerr 1995). The radiometric ages obtained by Mussett (1986) and Chambers and Pringle (2001) therefore indicate that the Mull floras are mid Paleocene in age.

The uppermost exposed section of the Mull lava field (700 m above sea level) at Ben Moire has provided an age of 59.05 ± 0.27 Ma (Chambers and Pringle 2001). These dates indicate that the Mull Lava Formation formed relatively rapidly within a maximum time interval of ~two million years. These dates are consistent with that of the Skye Lava Formation (see Chapter 2, section 2.3.3) which suggests both of these extensive lava formations are contemporaneous.

The palynomorph assemblages of the Ardtun Conglomerate Formation have been used by Jolley (1997) and Bell and Jolley (1997) to determine the age of this sequence, and like those of Skye, they differ from the radiometric dates. Jolley (1997) suggested an age of 55 to 54.5 Ma; this estimate places the sequence as latest Paleocene in age and associated with the Paleocene-Eocene Thermal Maximum (PETM). The rationale for dating the microfloras of Mull as PETM is based on the correlation with palynomorph assemblages of the West Shetland Basin and the lava composition of the Staffa Lava Formation (Jolley 1997, Bell and Jolley 1997). Multiple lines of evidence have been used for this younger age assignment and are outlined below:

a) The presence of pollen attributed to late Paleocene members of the Juglandaceae (*Caryapollenites*).

b) An abundance of *Ginkgo* pollen (*Monocolpopollenites tranquilus*) in the Mull palynofloras is shared with that of the West Shetland Basin.

c) The presence of several species of *Aquilapollenites*, which are present in the Eocene deposits of the West Shetland Basin.

d) Thoeliitic magma subtype of the Staffa Lava Formation, which is suggested as an indicator of lithospheric thinning associated with 'post rift' magmatism of the North Atlantic.

The dating based on the palynofloras has been questioned by Kerr and Kent (1998) who stated that study by Bell and Jolley (1997) did not incorporate the radiometric dating of Mussett (1986) as they considered these estimates to be unreliable. Kerr and Kent (1998) state that the estimates obtained by the Mussett (1986) study were reliable as they represent the true crystallisation ages of the basalt. The thoeliitic composition of the Staffa lavas was suggested by Bell and Jolley (1997) as being characteristic of lithospheric thinning caused by rifting of the North Atlantic during the latest Paleocene-Eocene. Kerr and Kent (1998) state that the theoliitic composition of the Staffa Lavas is not the result of lithospheric thinning but was the result of the assimilation of Moine crustal material and that originally the magmatic composition was similar to that of the overlying lavas of the Plateau Formation.

Comparisons were made between the palynomorph assemblages of Mull and those of the latest Paleocene sequences of the Cobham Lignite in southern England. Both palynofloras share many of the same plant taxa including *Inaperturopollenites*, *Platycaryapollenites* and *Triporopollenites*, suggesting that these plants were widespread in Britain during the Paleocene (Jolley 1997, Collinson et al. 2009). Thermophillic palynomorph taxa are relatively rare, with the exception of palm pollen in Cobham lignite (Collinson et al. 2009). Palynomorph taxa with theromophillic preferences including palm pollen are absent from the Mull flora. The climate during the late Paleocene was warm and humid and rapidly warmed at the PETM (Zachos et al. 2001), which is evident from in the Cobham lignite. Although there is no apparent extinction or immigration at the onset of the PETM there is a significant change in the community and climate. The palynoflora shifts from a fern and woody angiosperm, fire-prone community to a humid taxodiaceous and palm-dominated community (Collinson et al. 2009). Floristic change has been documented in palynofloras from the USA during the PETM (e.g. Harrington et al. 2004, Wing et al. 2005), which show an even more pronounced change. Jolley (1997) did not note a major change in the floral composition or community structure in Mull or the West Shetland Basin at this interval, which suggests that these floras are not latest Paleocene in age.

Based on the potential uncertainties with the palynological dating, the more accepted radiometric age of 60.5 ± 0.3 Ma (Chambers and Pringle 2001) is considered the best estimate of the age of the Ardtun Conglomerate Member. This date confirms the earlier study by Mussett (1986) and because this technique is less prone to interpretational errors and is more consistent with the chronological development of the BTVP as whole it is considered here as more reliable.

7.4 Fossil floras of Mull

7.4.1 Plant macrofossil diversity of Ardtun, Mull

The plant macrofossil record of Mull offers a useful opportunity to determine the vegetation composition of other leaf assemblages in the BTVP. Assessment of the Mull floras will also provide information on the variability in floral diversity and composition across the province. This study has not undertaken a taxonomic review of the Mull flora, but relies on the comprehensive study of Boulter and Kvacek (1989). Instead new observations during this project based on the collections housed in the National History Museum, London; the British Geological Survey, Keyworth; and the National Museums of Scotland, Edinburgh are incorporated with the study of Boulter and Kvacek (1989).

In total 24 plant species have been recognised from Ardtun and include two species of marchantiophytes (liverworts), two pteridophytes, five gymnosperms and fifteen angiosperms were present (Boulter and Kvacek 1989) (Table 7.1). The two species of marchantiophytes are represented by a single specimen each. Cuticular analysis of the fossil specimens revealed comparatively little regarding their higher taxonomic affinity except they may represent members of the orders Jugermanninales and Marchantities (Boulter and Kvacek 1989) (Table 7.1).

Pteridophyte fossils include the fern *Onoclea hebridica* and the sphenophyte *Equisetum* sp. Fossil fronds of *Onoclea hebridica* are well represented in the flora, and particularly abundant in the 'black leaf bed' and siltstone deposits. The presence of fern fossils in the assemblage indicates that flooding events occurred with sufficient energy to abcise the fronds.

The gymnosperm element of the Ardtun flora includes *Ginkgo* and conifers attributed to the Cupressaceae and Taxaceae. Fossilised leaves of *Ginkgo gardneri* are well preserved and display a wide range of lamina dissection patterns, from almost un-dissected to those with five or more lobes.

Cupressaceous conifer fossils include *Metasequoia occidentalis*, *Glyptostrobus dunoyeri* and the enigmatic *Elatocladus campbellii* (Table 7.1). Boulter and Kvacek (1989) suggested the morphology of *Elatocladus campbellii* was similar to that of *Sequoia*, but cuticular analysis revealed similarities to *Taxodium*. The specimens of *Elatocladus* from Ardtun are similar to those found on Skye, and indeed appear nearly identical. The presence of *Sequoia*-like ovulate cones on Skye confirms the tentative association of *Sequoia* to the specimens of *Elatocladus campbellii*, which Boulter and Kvacek (1989) considered to be most similar to this genus.

The Taxaceae are represented by a single sterile shoot species *Amentotaxus gladifolia* (Table 7.1), whose affinity with the Taxaceae is confirmed by cuticular characteristics, particularly the arrangement of the stomata (Ferguson et al. 1978). Fossil and modern representatives of this genus are associated with warm temperate or subtropical climates (Ferguson et al. 1978, Eckenwalder 2009), which suggests that this conifer was possibly growing in a similar climate regime.

Angiosperms are the most abundant and diverse component of the Ardtun flora with 14 leaf types recognised (Table 7.1, Figure 7.5). These angiosperms show similarities to families including the Platanaceae, Cercidiphyllaceae, Betulaceae, Fagaceae, Juglandaceae, Vitaceae and Cornaceae (Boulter and Kvacek 1989). Among the floras of Mull are a variety of angiosperm leaf types that are enigmatic. These leaf types include *Cupuliferites rubrifolius*, *Camptodromites major*, *Camptodromites multinervatus*, *Davidoidea hebridica*, *Davidoidea ardtunensis* and *Zizyphoides ardtunensis* (Table 7.1 and Figure 7.5). All but the latter form have been attributed to the Hamamelididae due to the absence of other pollen types attributed to the Fagales and their overall morphology (Boulter and Kvacek 1989).

Table 7.1. Plant macrofossils from Ardtun Mull, showing their family affinity and their relative abundance within the flora.

Taxon	Attributed family	Number of specimens	Relative abundance (%)	Abundance category
Pteridophyta				
Equisetum sp.	Equisetaceae	145	14.7	dominant
Onoclea hebridica	Dennstaedtiaceae	83	8.4	common
Gymnospermae				
Ginkgo gardneri	Ginkgoaceae	33	3.4	uncommon
Metasequoia occidentalis	Cupressaceae	7	0.7	rare
Elatocladus campbelli	Cupressaceae	36	3.7	uncommon
Glyptostrobus dunoyeri	Cupressaceae	13	1.3	uncommon
Amenotaxus gladifolia	Taxaceae	36	3.7	uncommon
Angiospermae				
Platanites hebridicus	Platanaceae	145	14.7	dominant
Trochodendroides antiqua	Cercidiphyllaceae	58	5.9	common
Corylites hebridicus	Betulaceae	142	14.4	dominant
Fagosiphyllum groenlandica	Fagaceae	14	1.4	uncommon
Cupuliferites rubrifolius	Hamamelididae	8	0.8	rare
Juglandiphyllites ardtunensis	Juglandaceae	3	0.3	rare
Juglandiphyllites finlayi	Juglandaceae	1	0.1	rare
Camptodromites major	Hamamelididae	72	7.3	common
Camptodromites multinervatus	Hamamelididae	95	9.7	common
Davidoidea hebridica	Hamamelididae	26	2.6	uncommon
Davidoidea ardtunensis	Hamamelididae	42	4.3	uncommon
Vitiphyllum sewardii	Vitaceae	7	0.7	rare
Zizyphoides ardtunensis	unknown	17	1.7	uncommon
Cornophyllum hebridicum	Cornaceae	1	0.1	rare

Abundance category = Rare <1%, uncommon 1-5%, common 5-10%, dominant >10%.

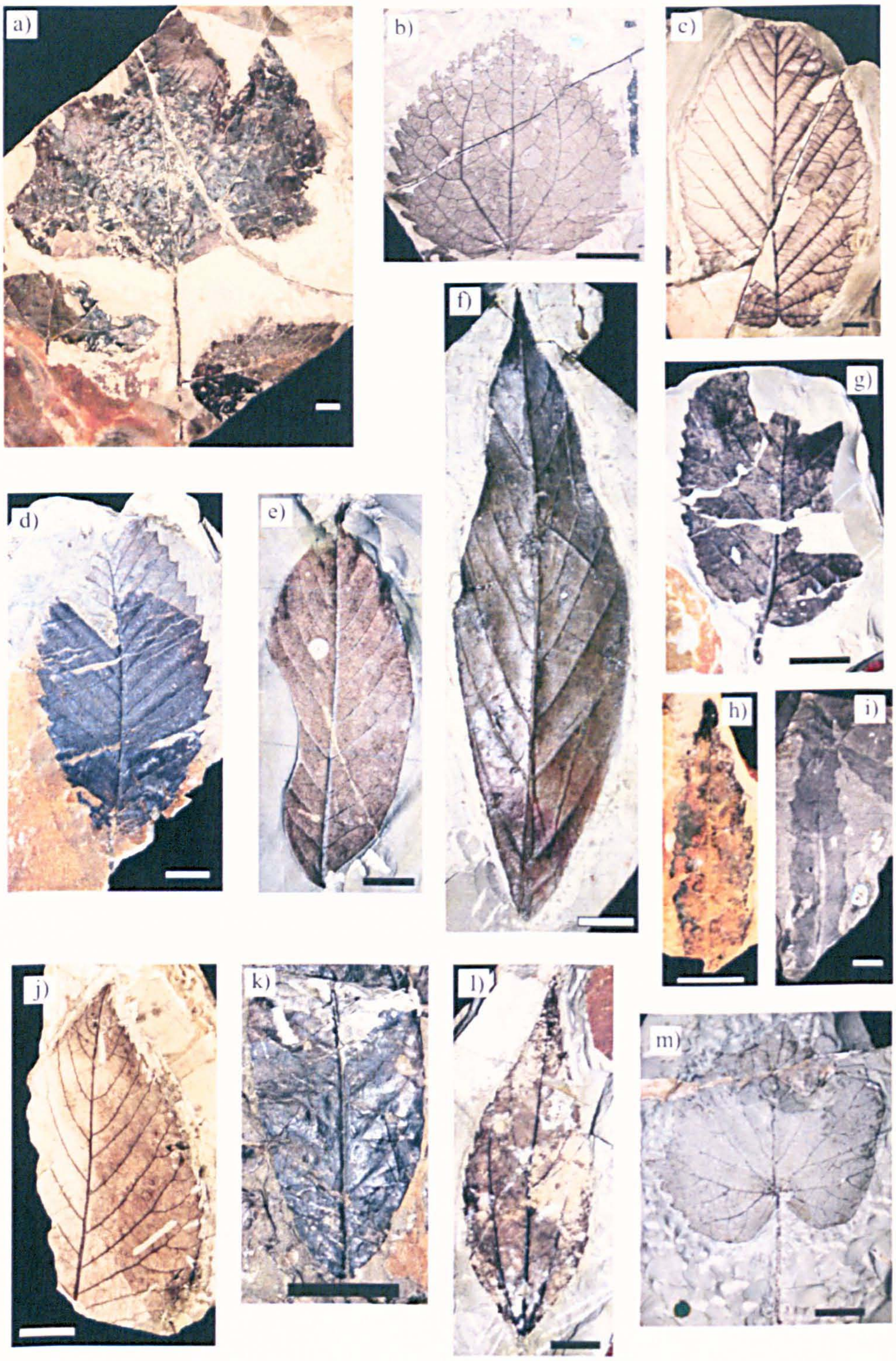

Figure 7.5. Fossil angiosperm leaves of Ardtun, Mull. a) *Platanites hebridicus* (V25040), b) *Trochodendroides antiqua* (V25164), c) *Corylites hebridicus* (V25080), d) *Fagopsiphyllum groenlandica* (V32357), e) *Juglandiphyllites ardtunensis* (V25133), f) *Camptodromites major* (V25122), g) *Davidoidea hebridica* (V25224), h) *Juglandiphyllites finlayii* (V26330), i) *Cupuliferites rubrifolius* (unregistered NHM), j) *Davidoidea ardtunensis* (PBT 214), k) *Camptodromites multinervatus* (V25073), l) *Zizyphoides ardtunensis* (V25144), m) *Vitiphyllum sewardii* (V25184). Scale bar = 1 cm.

7.4.2 Vegetation composition and structure

7.4.2.1 Relative abundance of floral elements

The relative abundance of the plant taxa within the Ardtun leaf beds and the growth habit of these plants will provide clues to the vegetation composition and structure of this flora. Counts of the fossil plant specimens were made from the London and Edinburgh collections to determine the relative abundance of each plant type within the flora. In total 984 individual plant macrofossil specimens were identified and counted. Angiosperm leaf fossils are the most abundant component of the collections and represent 64.1% of the specimens, pteridophyte fossils account for 23.2% and the gymnosperms are the least abundant with 12.7% (Figure 7.6).

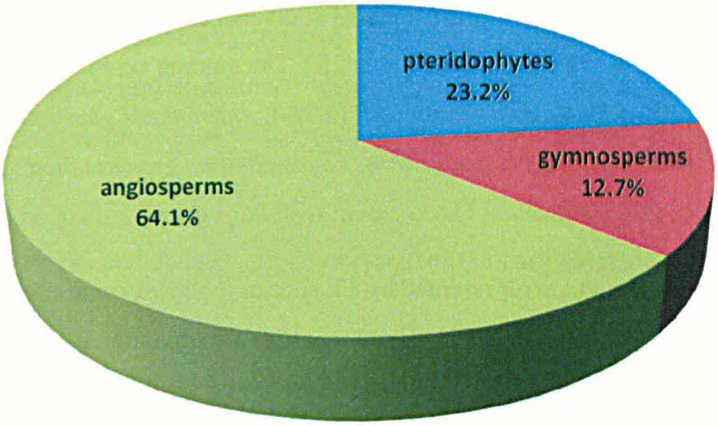

Figure 7.6. Relative abundance of pteridophytes, gymnosperms and angiosperms in the collections of the Ardtun flora of Mull.

The relative abundance of angiosperms in the collections indicates these were the dominant floral element of the vegetation. The pteridophytes would have grown in disturbed environments, in the understory or in the margins of the angiosperm-dominated vegetation. The relative rarity of gymnosperms suggests these components of the flora were sparsely distributed in the vegetation or grew away from the site of deposition.

It is important to note that the specimens in the fossil collections may be selective and not representative of the original source flora. This may be of particular significance to the angiosperm fossils which may have been selectively collected for complete, well preserved or rare species; these taxa may therefore be overrepresented in the collections. It is difficult to account for this potential bias, but the rarity of the conifer fossils appears to be genuine. Conifer shoots are highly abundant in the Allt Mor flora of Skye and occur on surfaces with angiosperm leaves. The scarcity of conifers in the Ardtun flora even on larger slabs of >200mm slabs indicates these plants were rare floral elements. Conifer pollen is also relatively uncommon in the sediments from Ardtun (Jolley et al. 2009), which suggests these plants were growing away from the site of deposition.

The counts for individual leaf taxa indicates that there is significant variation in the relative abundance of each plant type within the Ardtun flora (Table 7.1, Figure 7.7). The relative abundance of taxa was converted into abundance categories to establish which elements were dominant (>10%), common (5-10%), uncommon (1-5%) or rare (<1%).

Dominant elements of the flora include *Equisetum* sp (14.7%), *Platanites hebridicus* (14.7%) and *Corylites hebridicus* (14.4%) (Table 7.1, Figure 7.7). Common components include *Camptodromites multinervatus* (9.7%), *Onoclea hebridica* (8.4%), *Camptodromites major* (7.3%) and *Trochodendroides antiqua* (5.9%).

Uncommon components of the collection represent the most diverse component of the flora and collectively account for 22.1% of the specimens (Figure 7.7). Uncommon taxa include *Davidoidea ardtunensis* (4.3%), *Elatocladus campbellii* (3.7%), *Amenotaxus gladifolia* (3.7), *Ginkgo gardneri* (3.4%), *Davidoidea hebridica* (2.6%), *Fagosiphyllum groenlandica* (1.4%) and *Glyptostrobus dunoyeri* (1.3%) (Table 7.1).

Rare floral elements are diverse and are represented by six species, collectively accounting for a small percentage (2.7%) of the flora (Figure 7.7). These rare taxa are primarily angiosperms (Table 7.1) but also include the conifer *Metasequoia occidentalis* (0.7%).

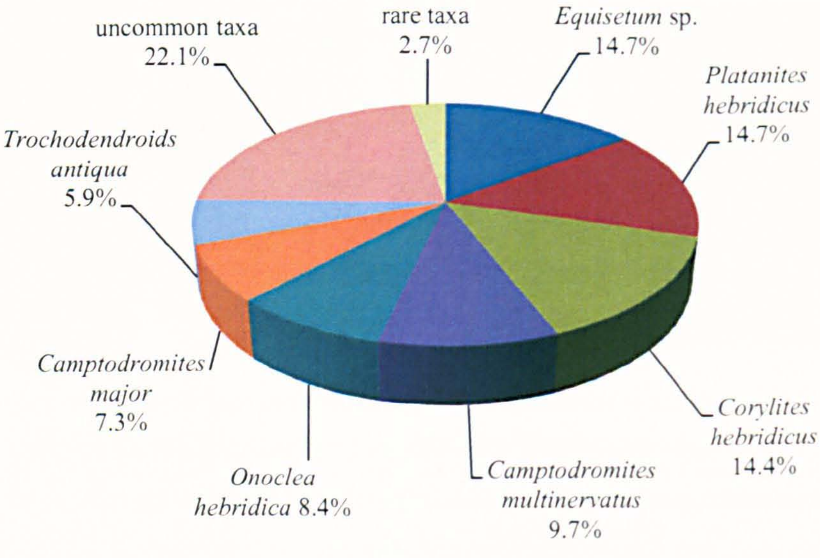

Figure 7.7. Relative abundance of plant macrofossil taxa within the Ardtun flora of Mull.

7.4.2.2 Vegetation structure

Sedimentological, macrofossil and palynological evidence indicates that the palaeoenvironmental conditions and community structure of Ardtun were variable. The presence of facies associated with fluvial, lacustrine and swamp environments suggests flood regimes influenced the depositional environment and the vegetation that colonised and developed.

Counts of specimens were made from the Natural History Museum, London collection from each rock sample. The rock samples lithology and the number of each plant taxon were recorded. Five broad lithologies were recognised and included fine grained sandstones, siltstones, mudstone/clay, fine grained limestone and black siltstone. Samples with sandstone and siltstone lithologies were grouped, as these sediments appear to represent fluvial deposits. The mudstone/clays and limestone lithologies were grouped as these sediments appear to reflect overbank or lacustrine deposition. The black shale samples were grouped as these appear to correspond to the 'black leaf bed', which is attributed to swamp conditions.

These lithological groupings and their associated plant macrofossils appear to reflect three broad community types and include a riparian community, marginal pond/lake community and a swamp community (Table 7.2).

The riparian community is based on sandstone and siltstone lithologies that represent marginal fluvial deposition. This community type is the most diverse with 18 species present; however, the majority of these are low in abundance (Table 7.2, Figure 7.8). The high diversity of this community and the low relative abundance may represent a taphonomic artefact. The fluvial origin of these sediments indicates that some of the plant material may have been transported and washed into these depositional sites (allochthonous origin), which could account for the high diversity and rarity of some of the taxa. The most abundant taxa within this community include *Equisetum* sp., *Onoclea hebridica*, *Platanites hebridicus*, *Camptodromites major*, *Corylites hebridicus* and *Ametotaxus gladifolia* (Table 7.2, Figure 7.8). The lithology and flora of this community type is indicative of disturbed conditions related to flooding.

Equisetum sp. and *Onoclea hebridica* may represent early colonisers of newly developed flooding surfaces. The habit of the Mull fern foliage and their association with flood deposits has been observed in the related taxa, *Onoclea sensibilis* from the Paleocene of Alberta. This related species appears to have been a coloniser of flooding surfaces along with *Metasequoia* and *Palaeocarpinus* (Betulaceae) (Rothwell and Stokey 1991). As flooding intensity or frequency waned the angiosperms *Platanites hebridicus*, *Camptodromites major* and *Corylites hebridicus* would have developed in these environments, possibly along with the shrubby conifer *Ametotaxus gladifolia*.

Table 7.2. Community types represented by the leaf macrofossils of the Ardtun flora of Mull, their lithology, associated taxa and relative abundance within the community.

Community type	Lithology	Associated taxa	Relative abundance (%)
Riparian Community	Silstones and sandstones	*Equisetum* sp.	26.5
		Onoclea hebridica	18.8
		Platanites hebridicus	14.3
		Camptodromites major	8.1
		Corylites hebridicus	7.0
		Amenotaxus gladifolia	4.8
Marginal lacustrine community	Limestone and claystones	*Corylites hebridicus*	23.7
		Trochodendroides antiqua	11.5
		Camptodromites major	10.2
		Platanites hebridicus	9.9
		Davidoidea ardtunensis	8.6
		Elatocladus campbelli	6.8
		Davidoidea hebridica	6.8
		Ginkgo gardneri	6.3
		Amenotaxus gladifolia	6.0
Swamp Community	Black shale	*Camptodromites multinervatus*	45.3
		Platanites hebridicus	20.7
		Equisetum sp.	17.9
		Onoclea hebridica	8.9
		Elatocladus campbelli	3.9
		Glyptostrobus dunoyeri	2.2
		Corylites hebridicus	1.1

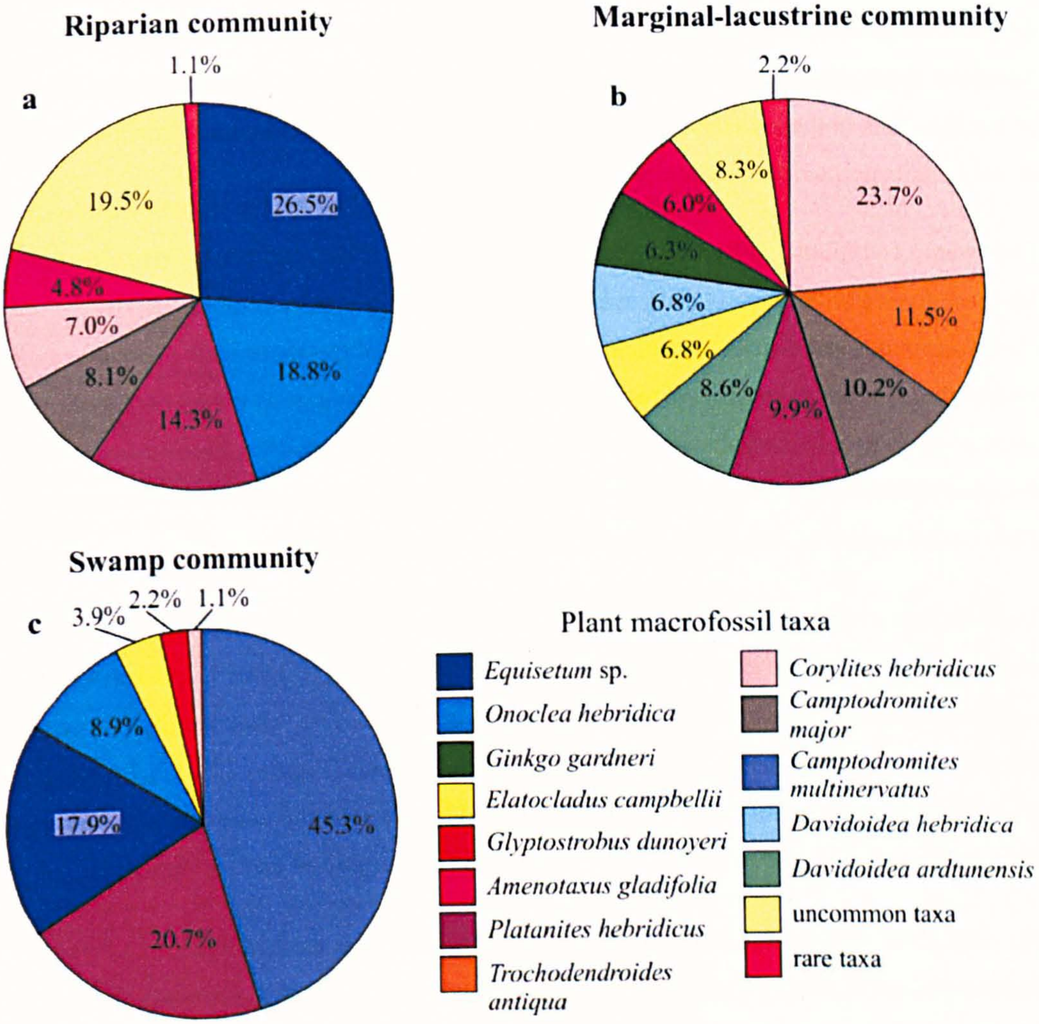

Figure 7.8. Floral communities of Ardtun Mull, showing the plant taxa present within each community and their relative abundance.

The marginal lacustrine community is based on fine grained clay and limestone deposits and the leaf fossils preserved in these sediments. These sediments appear to correspond with the steel grey clays and limestone beds of the second ravine section at Ardtun head (Figure 7.4). These sediments are interpreted as overbank sediments that were deposited into a swampy/lacustrine setting on the lava surface.

This community contains 17 plant species, primarily angiosperms but *Ginkgo* and conifers are relatively common (Table 7.2, Figure 7.8). The most abundant components of this community include *Corylites hebridicus*, *Trochodendroides antiqua*, *Camptodromites major*, *Platanites hebridicus* and *Davidoidea ardtunensis*. This community shares many of the same taxa with that of the riparian community and indeed the marginal community may represent an advanced seral stage typified by lower disturbance. The limestone deposits may indicate that relatively calm water conditions with little clastic input, which is suggested by the absence of *Equisetum* and the scarcity of *Onoclea* (0.3%). The plant fossils in these lacustrine facies appear to represent the local marginal environment, and the leaves may not been transported far prior to their depostion (parautochthonous assemblage). The high floral diversity and high relative abundance of multiple taxa in these sediments suggests that the margins of these ponds or lakes supported a diverse angiosperm-rich community.

The swamp community is based on the black shales of the 'black leaf bed'. This community is the least diverse with seven plant species recorded. This community is dominated by *Camptodromites multinervatus*, which accounts for 45.3% of the specimens. *Camptodromites multinervatus* is largely restricted to this lithological unit and suggests it may have been swamp plant or an early coloniser of swampy conditions. *Platanites hebridicus*, *Equisetum sp.* and *Onoclea hebridica* are common members of this community type, with rare occurrences of *Elatocladus campellii*, *Glyptostrobus dunoyeri* and *Corylites hebridcus*.

The lithology of this community is based on the samples of the suspected 'black leaf bed', which occurs in all three exposures of the Ardtun Conglomerate (Figures 7.2, 7.3, 7.4), this suggests that this swamp environment was laterally extensive. The 'black leaf bed' appears to represent a channel fill deposit as it rests upon channel gravels (Figures 7.2, 7.3, 7.4). The low diversity of this community may be partly explained by the potential authochtonous origin of the deposit, which would have reduced the potential for transported leaf material.

The high water table of this channel fill may have prevented the establishment of a diverse community, or the interval between flooding events was too short for community development. The vegetation structure of this community may have been relatively open, with a herbaceous ground layer of *Equisetum* and *Onoclea* with shrubby angiosperms such as *Camptodromites multinervatus* and *Platanites* interspersed with water tolerant conifers such as *Glyptostrobus* and *Elatocladus*.

7.5 Climate analysis of the Paleocene floras of Mull

The fossil floras of Ardtun, Mull provide an opportunity to further access the palaeoclimate of the BTVP during the mid Paleocene. This flora has not been quantifiably used for palaeoclimate analysis, and therefore the results in this study will provide the first estimates of the palaeoclimate. The angiosperm leaf fossils of Mull were scored according to the same methodology as outlined in Chapter 6 (see 6.2.2). Fourteen angiosperm leaf types were recognised by Boulter and Kvacek (1989), and these appear to represent valid leaf morphotypes.

The angiosperm leaf fossils are dominated by toothed types, with entire margined species represented by only three taxa (*Camptodromites major*, *Camptodromites multinervatus* and *Cornophyllum hebridicum*) (Table 7.3). *Davidoidea ardtunesis* possess teeth that are considered spinose. Wolfe (1993) stated that spinose teeth represent an adaption against insect herbivory rather than an adaption to climate and should be scored as entire. Specimens of *Davidoidea ardtunesis* have spinose and serrate teeth and have therefore been scored as being both toothed and entire (score 0.5).

Table 7.3. Angiosperm taxa of Ardtun, Mull showing their margin type.

Angiosperm taxon	Margin toothed	Margin entire
Platanites hebridicus	X	
Trochodendroides antiqua	X	
Corylites hebridicus	X	
Fagiosiphyllum groenlandica	X	
Cupuliferites rubrifolius	X	
Juglandiphyllites ardtunensis	X	
Juglandiphyllites finlayi	X	
Camptodromites major		X
Camptodromites multinervatus		X
Davidoidea hebridica	X	
Davidoidea ardtunensis	X	X
Vitiphyllum sewardii	X	
Zizyphoides ardtunensis	X	
Cornophyllum hebridicum		X

The angiosperm leaf taxa were also scored for the 31 leaf character states for CLAMP and MLR analysis (see Chapter 6, section 6.2.2). The flora is dominated by unlobed, toothed leaves, leaves with lamina sizes ranging from microphyll II to mesophyll III, acute and attenuate apexes, all base shapes particularly acute, leaves with L:W of 1-2:1 to 3-4:1 and elliptic lamina shapes (Table 7.4.).

The margin percentage of the Mull flora (25%) (i.e. the percentage of the flora with entire margins) and the combined floral score for the 31 physiognomic characters were used to establish the palaeoclimate for Mull using LMA, CLAMP and MLR models. The procedure and methods used were the same as those applied to the Skye flora (see Chapter 6, sections 6.2.3, 6.2.4, 6.2.5). The sampling error for the LMA equations was carried out according to Wilf (1997), (see Chapter 6, section 6.3.1). The estimates obtained from the three physiognomic methods indicate that the palaeoclimate for Mull was warm, seasonal and humid (Table 7.5).

Table 7.4. Leaf physiognomic characters scored for the Ardtun flora of Mull.

leaf character	percentage	leaf character	percentage
lobed	3.5	apex shape: emarginate	0
no teeth (entire margin)	25	apex shape: round	4
teeth regular	30	apex shape: acute	64
teeth close	45	apex shape: attenuate	32
teeth round	41	base shape: cordate	29
teeth acute	27	base shape: round	29
teeth compound	11	base shape: acute	42
lamina size: nanophyll	0	lamina length:width <1:1	17
lamina size: leptophyll I	0	lamina length:width 1-2:1	25
lamina size: leptophyll II	0	lamina length:width 2-3:1	25
lamina size: microphyll I	0	lamina length:width 3-4:1	29
lamina size: microphyll II	34	lamina length:width >4:1	4
lamina size: microphyll III	25	lamina shape: obovate	0
lamina size: mesophyll I	17	lamina shape: elliptic	82
lamina size: mesophyll II	12	lamina shape: ovate	18
lamina size: mesophyll III	11		

For definitions of these character states see the CLAMP website (http://clamp.ibcas.ac.cn)

Table 7.5. Climate estimates derived from the physiognomic analysis of the mid Paleocene floras of Mull using LMA, CLAMP and MLR models.

Model	MAT (°C)	SE	CMM (°C)	SE	WMM (°C)	SE	MART (°C)	SE	GSL (months)	SE	GSP (mm)	SE	MMGSP (mm)	SE	3WET (mm)	SE	3DRY (mm)	SE
LMA1	8.8	3.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA2	9.4	3.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA3	7.0	3.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA4	11.3	4.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA5	8.4	3.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA6	8.6	3.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LMA7	7.9	3.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CLAMP1	11.0	1.7	0.3	3.0	22.0	1.8	-	-	6.6	0.8	1525	194	214	25	827	133	244	35
CLAMP2	12.5	1.8	3.0	2.6	22.6	1.8	-	-	7.5	0.9	2022	317	259	37	988	137	621	89
CLAMP3	11.4	1.1	0.9	1.9	22.6	1.4	-	-	6.8	0.7	1550	200	218	26	847	146	233	32
CLAMP4	13.0	1.2	2.9	1.9	24.2	1.6	-	-	7.8	0.7	2117	331	274	31	1035	141	698	104
MLR1	8.0	2.0	-2.5	3.6	23.9	2.9	14.6	5.0	-	-	1263	472	-	-	-	-	230	89
MLR2	5.2	2.7	-5.9	3.5	26.5	2.5	33.7	3.8	-	-	1476	300	-	-	-	-	-	-
MLR3	10.0	2.0	-	-	-	-	-	-	-	-	1809	512	-	-	-	-	-	-

MAT = mean annual temperature, SE = standard error, CMM = cold mean month temperature, WMM = warm mean month temperature, MART = mean annual range in temperature, GSL = growing season length, GSP = growing season precipitation, MMGSP mean monthly growing season precipitation, 3WET = three wet month precipitation, 3DRY = three dry month precipitation, - = transfer function not available to determine this particular climatic variable.

7.5.1 Mean annual temperature estimates

The MAT estimates derived from the Mull flora are indicative of temperate to warm temperate climates (Wolfe 1979). The estimates derived from CLAMP are the warmest (excluding LMA4) and range from 9.3 °C to 14.2 °C (mean 12.0 °C) (Tables 7.5, 7.6). The CLAMP estimates indicate that the climate was warm-temperate, and close to or above the microthermal-mesothermal boundary at 13°C (Wolfe 1979).

The LMA estimates range from 3.6 °C to 15.5 °C (mean 8.9 °C). The substantial range of 11.9 °C for this method is related to the high sampling error. The Mull floras has a low diversity with 14 leaf types and a the margin percentage of 25%, which has resulted in a high sampling error ranging from 3.2 °C to 4.2 °C, which is consistent with the findings of Wilf (1997) (Table 7.5). The MAT estimates derived from the MLR models are the coolest obtained and range from 2.5 °C to 12 °C (mean 7.7 °C) (Tables 7.5, 7.6). Both the LMA and MLR estimates are in close agreement and indicate that the climate was temperate to warm temperate during the mid Paleocene.

The MAT estimates derived from LMA and MLR, although cooler than CLAMP, are comparable when the sampling error/standard error is taken into account, which suggests that the climate may be more comparable with that of a warm temperate climate.

Table 7.6. Mean annual temperature (°C) estimates derived from LMA, CLAMP and MLR analyses showing minimum, maximum, mean and range of the estimates.

Physiognomic method	min	max	mean	range
LMA	3.6	15.5	8.9	11.9
CLAMP	9.3	14.2	12.0	4.9
MLR	2.5	12	7.7	9.5

7.5.2 Seasonality

Cold mean month temperature estimates derived from CLAMP and the MLR models indicates that the winter months were cool. The CLAMP estimates of CMM are appreciably warmer than the MLR estimates and range from -2.7 °C to 5.6 °C (mean 1.8 °C) and -9.4 °C to 1.1 °C (mean -4.2 °C) respectively (Tables 7.5, 7.7). The estimates derived from the MLR models like those derived from the Skye floras appear to be unrealistically cold for the mid Paleocene. The CLAMP estimates indicate the winters were cool and frosts may have occurred, but may have been infrequent.

The presence of a possible notophyllous evergreen species within the Mull flora, *Camptodromites major*, indicates that the CMM may have been above 1°C, which is the modern threshold for plants with this physiognomy (Wolfe 1979). The low diversity of leaves with this physiognomy does suggest that the CMM may not have been much greater than 1 °C however, which is constant with the CLAMP estimates.

The estimates for WMM derived from the CLAMP and MLR models are comparable, with a range of 20.2 °C to 25.8 °C (mean 22.4 °C) and 21 °C to 29 °C (mean 25.2 °C) respectively (Tables 7.5, 7.7). These estimates of WMM suggest that the summer temperatures were warm and when compared with the CMM estimates the climate of Mull during the mid Paleocene appears to have been moderately seasonal.

Table 7.7. Cold mean month (°C) and warm mean month (°C) estimates derived from CLAMP and MLR analyses showing minimum, maximum, mean and range of the estimates.

Cold mean month temperature (°C)				
Physiognomic method	min	max	mean	range
CLAMP	-2.7	5.6	1.8	8.3
MLR	-9.4	1.1	-4.2	10.5
Warm mean month temperature (°C)				
Physiognomic method	min	max	mean	range
CLAMP	20.2	25.8	22.4	5.6
MLR	21.0	29.0	25.2	8.0

7.5.3 Precipitation

Estimates of GSP derived from CLAMP and the MLR models have produced highly variable values, with large ranges when sampling error is taken into account. CLAMP produced a range of 1331 mm to 2448 mm (mean 1804 mm) and the MLR models range from 791 mm to 2321 mm (mean 1516 mm) (Tables 7.5, 7.8). As noted in Chapter 6 (see section 6.3.2) the estimates of GSP produced by CLAMP1 and CLAMP3 may be unreliable for this parameter. The the estimates produced by CLAMP2 and CLAMP4 are 2022 ± 317 mm and 2117 ± 331 mm respectively, which indicates a humid climate state. The GSP estimates derived from the MLR models are generally drier than CLAMP2 and CLAMP4 but do overlap with these latter estimates.

Table 7.8. Growing season precipitation (mm) estimates derived from CLAMP and MLR analyses showing minimum, maximum, mean and range of the estimates.

Physiognomic method	min	max	mean	range
CLAMP	1331	2448	1804	1117
MLR	791	2321	1516	1530

Estimates of 3WET and 3DRY month precipitation from CLAMP indicate precipitation may have been mildly seasonal. CLAMP2 and CLAMP4 estimate 3WET to have been 988 ± 137 mm and 1035 ± 141 mm respectively, and for 3DRY the estimates are 621 ± 89 mm and 698 ± 104 mm. These results indicate that precipitation patterns may have fluctuated annually, but are not indicative of seasonally arid or monsoonal conditions.

As discussed in Chapter 6 (see section 6.4.3) precipitation estimates derived from physiognomic techniques in mesic environments are typically inaccurate. This prevents an accurate assessment of the past precipitation of Mull, but the high values derived CLAMP and the MLR models suggest that the climate was humid and comparable with modern temperate rainforest conditions (Alaback 1991).

7.5.3 Potential sources of error

The palaeoclimate estimates derived from the fossil floras of Ardtun, Mull, like those of Skye, may be influenced by a variety of taphonomic and environmental factors. As noted in section 7.5.1 low floral diversity has resulted in high sample error for the MAT estimates derived from the LMA equations. This factor cannot be readily reconciled but does suggest that the low angiosperm diversity of Skye is a genuine ecology signal rather than a taphonomic bias and that floras of the BTVP were relatively impoverished.

The fossil angiosperm leaves of Mull are exceptionally well preserved and a high proportion of the leaf types have specimens with complete preservation, and in many cases with high order venation present (Figure 7.6). A detailed analysis of leaf preservation for the Mull flora was not taken in this study, but the completeness score for the 31 character traits for the CLAMP analysis is 0.91. This translates to 91% of the traits being scored for the whole flora, which indicates that the physiognomic analysis is less affected by missing data, and the estimates obtained from CLAMP and MLR are more reliable.

The wide variety of depositional environments represented by the sediments and floras of the Ardtun Conlgomerate Formation may have mitigated the effects taphonomy has on climate signals obtained from fossil leaf assemblages. The floras of Mull were deposited in a variety of palaeoenvironments attributed to fluvial, lacustrine and swamp conditions, which in turn represent allochthonous, parautochthonous and autochthonous leaf assemblages. These depositional environments and leaf assemblages are likely to better preserve the overall floral diversity and composition as they are likely to capture different aspects of the overall flora. The varied facies types present at Ardtun and the multiple environments and plant communities they represent should provide a more representative climate signal.

The effects of saturated soils on floral composition and physiognomy was discussed in Chapter 6 (see section 6.4.4.2). This factor may have influenced the MAT signal from the Mull floras as they grew in partially or fully saturated conditions. Kowlaski and Dilcher (2003) noted that in wet soil sites in Florida there were higher proportion of toothed woody dicots compared to coeval drier sites. This phenomena does not appear to apply directly to the Mull flora, as *Camptodromites multinervatus*, an entire margined leaf type is almost exclusively restricted to the swamp facies of the 'black leaf bed'. This one exception may suggest this effect may be less important for the floras of the BTVP.

7.5.4 Climate summary

The climate estimates obtained from the fossil angiosperms of the Ardtun flora of Mull indicate that the climate was a humid warm-temperate, seasonal, with cool to mild winters and warm summers. The interpretations of the palaeoclimate of the Mull flora by previous authors have suggested that the climate was humid warm-temperate to subtropical (Boulter and Kvacek 1989, Jolley 1997). The results from this study suggest that a subtropical climate is unlikely but may have been at the upper end of the warm-temperate, and close to the micro-mesothermal boundary (MAT 13°C) (Wolfe 1979). The estimates from this study also suggest that the flora of Mull was growing in a warm-temperate, but may have been close to being subtropical, which is relatively consistent with the findings from previous studies.

7.6 The fossil floras and climate of Mull and Skye: a comparison

The fossil floras of Mull and Skye offer an opportunity to determine the floristic composition of the BTVP at more regional scales as well as providing a broader understanding of the climate of the mid Paleocene for this region. Comparisons are made regarding their relative ages, their floral diversity, their vegetation composition and the palaeoclimate signals obtained for each of the floras.

7.6.1 Comparison of the relative ages of the Mull and Skye floras

The relative age of these two floras has important implications for the comparisons that can be made of the floral composition and climate estimates. If the floras are of different ages it could account for any differences observed between them. The palynological dating of these two floras suggests that the floras of Skye are 58.23 to 57.99 Ma and floras of Mull are 55 to 54.5

Ma (Jolley 1997, Bell and Jolley 1997). As discussed in Chapter 2 (see section 2.5.1 and earlier in this chapter (see section 7.2) the palynological dates are considered unreliable estimates.

The radiometric dates of the two floras indicate that they are mid Paleocene in age 60.5 ± 0.3 Ma (Ardtun flora) and 60.16 ± 0.45 Ma (Allt Mor flora) (Hamilton et al. 1998, Chambers and Pringle 2001). The margin of error of these dates, however, could suggest these floras were not contemporaneous, which is supported by field relationships.

The Staffa Lava Formation and the Ardtun plant beds contained within these lavas are stratigraphically below those of the thicker Plateau Lava Formation. The Mull Plateau lavas are compositionally similar and appear to represent a similar eruption style to those of Skye, and based on their radiometric dating appear to have formed contemporaneously (Chambers and Pringle 2001). This is also confirmed by the magmatic composition of the Staffa lavas, which are tholeiitic, and therefore may correspond to early phases of volcanism of the BTVP (Kerr 1998). Similar eruptions in Northern Skye at the base of the Skye Lava Formation may correspond with those of Staffa (Kerr 1998), which suggests this style of volcanism may be characteristic of the early phases of BTVP volcanism.

The Allt Mor floras are situated well within the plateau-style lavas of the Skye Lava Formation (see chapter 2, section 2.2), which suggests they are more contemporaneous with that of the Plateau Formation of Mull than the Staffa Formation eruptions. Although the radiometric dates do overlap there is a possibility that the Ardtun floras could be 0.4 to 1 million years older than those of Allt Mor. Floristic and climatic differences observed in these floras could therefore be result of transient changes in the mid Paleocene climate.

7.6.2 Comparison of floral diversity and composition

The floras of Mull and Skye are close geographically, are both mid Paleocene in age and both developed in similar environments in a volcanic landscape. The floral compostion should therefore be approximately similar. In terms of overall diversity the two floras are comparable since Mull has 24 leaf macrofossil types and Skye has 22, which suggests that the floral diversity of the BTVP was relatively low.

Both floras share many of the same taxa, particularly the angiosperm elements (Tables 7.9, 7.10). Conifers that occur in both floras include *Metasequoia occidentalis* (CM1), *Elatocladus campbellii* (CM2) and *Glyptostrobus dunoyeri* (CM3). Angiosperms that occur in both floras include *Platanites hebridicus* (AM1), *Trochodendroides antiqua* (AM2), *Corylites hebridicus* (AM3), *Fagosiphyllum groenlandica* (AM5), *Vitiphyllum sewardii* (AM9) and *Cornophyllum hebridicum* (AM10). The family association of these angiosperms is similar for both floras, with representatives from the families Platanaceae, Cercidiphyllaceae, Betulaceae, Fagaceae, Jugladanceae, Vitaceae and Cornaceae occurring in both sites (Table 7.10).

Table 7.9. Families and species/morphotypes of Marchantiophytes, pteridophytes and gymnosperms present in the floras of Mull and Skye.

Order/family	Species/morphotype	Present on Mull	Present on Skye
Marchantiophyta			
Jungermanniales	*Jungermanniopsis* sp.	X	
Marchantiales	*Marchantities* sp	X	
Pteridophyta			
Equisetaceae	*Equisetum* sp.	X	
Dennstaedtiaceae	*Onoclea hebridica*	X	
Gymnospermae			
Ginkgoaceae	*Ginkgo gardneri*	X	
Cupressaceae	CM1 *Metasequoia occidentalis*	X	X
Cupressaceae	CM2/*Elatocladus cambelli*	X	X
Cupressaceae	CM3 *Glyptostrobus dunoyeri*	X	X
Cupressaceae	CM4 "*Chamaecyparis* cf."		X
Cupressaceae	CM5 "*Thuja* cf."		X
Cupressaceae	CM6 "*Mesocyparis* cf."		X
Cupressaceae	CM7 *Calocedrus* sp.		X
Pinaceae	CM8		X
Taxaceae	*Amentotaxus gladifolia*	X	

CM = conifer morphotype (Skye flora)

The two floras do however, differ markedly in their composition, with many types present in one flora and not the other. The Skye flora includes cupressaceous conifers (CM4-7) and a single species attributed to the Pinaceae (AM8). The Mull flora lacks any conifers associated to Cupressaceae (excluding taxodiceous types) or the Pinaceae, but includes gymnosperm elements not present in the Skye floras. *Ginkgo* and the Taxaceae conifer *Amentotaxus gladifolia* are relatively uncommon members of the Mull flora (Table 7.1), which are completely absent from the plant beds of Skye examined in this study. Pollen attributed to these two gymnosperms (Jolley 1997), as well leaves of *Ginkgo* found in Northern Skye (Anderson and Dunham 1964) suggest that these plants were present on Skye, but have not been preserved in the leaf beds of Allt Geodh' a' Ghamhna, Allt Mor and Glen Osdale.

The Mull flora also includes herbaceous elements including *Equisetum* and *Onoclea*, which are absent from the leaf beds of Skye. Their absence in the Skye floras may represent a taphonomic bias as these taxa are often preserved in higher energy flood deposits.

Although the two floras share six of the same angiosperm taxa they do differ markedly (Table 7.10). Angiosperms present exclusively to the Mull flora include *Cupuliferites rubrifolius*, *Juglandiphyllites ardtunensis*, *Juglandiphyllites finlayi*, *Camptodromites major*, *Camptodromites multinervatus*, *Davidoidea hebridica*, *Davidoidea ardtunensis* and *Zizyphoides ardtunensis*. It is possible however, that some of these taxa may be represented by some of the morphotypes on Skye. *Juglandiphyllites ardtunesis* and *Juglandiphyllites finlayi* as discussed in Chapter 3 (see sections 3.13 and 3.14) may potentially be the same species or closely related to AM6 and AM7 of Skye.

Table 7.10. Angiosperm families and species/morphotypes present in the Mull and Skye floras.

Order/family	Species/morphotype	Present on Mull	Present on Skye
Platanaceae	AM1 *Platanites hebridicus*	X	X
Cercidiphyllaceae	AM2 *Trochodendroides antiqua*	X	X
Betulaceae	AM3 *Corylites hebridicus*	X	X
Betulaceae	AM4 "*Corylites* cf."	?	X
Fagaceae	AM5 *Fagopsiphyllum groenlandica*	X	X
Hamamelididae	*Cupuliferites rubrifolius*	X	
Juglandaceae	AM6 Juglandiphyllites sp.1		X
Juglandaceae	AM7 Juglandiphyllites sp.2		X
Juglandaceae	AM8 "*Platycarya* cf."		X
Juglandaceae	*Juglandiphyllites ardtunensis*	X	
Juglandaceae	*Juglandiphyllites finlayi*	X	
Hamamelididae	*Camptodromites major*	X	
Hamamelididae	*Camptodromites multinervatus*	X	
Hamamelididae	*Davidoidea hebridica*	X	
Hamamelididae	*Davidoidea ardtunensis*	X	
Vitaceae	AM9 *Vitiphyllum sewardii*	X	X
Cornaceae	AM10 *Cornophyllum hebridicum*	X	X
unknown	*Zizyphoides ardtunensis*	X	
unknown	AM11 *Zizyphoides flabella*		X
unknown	AM12		X
unknown	AM13		X
unknown	AM14		X

AM = angiosperm morphotype (Skye flora), ? = possibly present

7.6.3 Comparison of vegetation structure

As outlined in the previous section the two floras share some similar floral components but each floral has taxa that are exclusive to each. The two floras also have markedly different vegetation structures. The Allt Mor flora of Skye is dominated by taxodiaceous and cupressaceous conifers, with common occurrences of angiosperms such as *Corylites*, *Platanities* and *Trochodendroides*. The Ardtun flora of Mull is dominated by angiosperms, most notably

Platanities, *Corylites*, *Camptodromites multinervatus* and *C. major*. Herbaceous elements including *Equisetum* and *Onoclea* are also common. In contrast to the Skye flora, conifers are typically uncommon, with *Amentotaxus* and *Elatocladus* being the most abundant forms.

The depositional setting of these floras may be a significant factor, which could account for their different vegetation structures. The Allt Mor flora developed in a palaeovalley which was drained by a braided river system and the distal floodplains, swamps and valley sides were dominated by climax conifers such as *Sequoia* (*Elatocladus*-type) and *Metasequoia*, along with cupressaceous conifers such as *Chameacyparis* and *Thuja*. The valley sides and tops may have supported stands of pines with members of the Cupressaceae. In the understory and margins of this conifer-dominated vegetation angiosperms were common, most notably *Platanites*, *Corylites* and *Trochodendroides*.

The Ardtun flora of Mull developed on an alluvial fan with rivers, floodplains and localised swamp and lake development (Kerr and Kent 1995, Jolley et al. 2009). The Mull flora appears to represent three community types: a riparian community with herbaceous pteridophytes and angiosperms, an angiosperm dominated marginal lacustrine community and an open pteridophyte-angiosperm-taxodiaceous conifer swamp community. The relatively rarity of conifers within the Ardtun flora may be related to the more disturbed depositional setting. This is confirmed by the palynological record which supports this assertion as their pollen is relatively uncommon component of the palynofloras of Ardtun (Jolley et al. 2009).

These two floras, to a certain extent, grew in similar fluvial dominated palaeoenvironments. The Ardtun flora of Mull may have developed in a more disturbed setting, which prevented the establishment of climax conifers, or may represent a shorter quiescent interval between eruptions. The Allt Mor flora of Skye may represent a more mature ecosystem that either had a longer period for development or suffered less intense disturbance during its development.

The ambient climatic conditions that the two floras grew in may also be responsible for apparent differences in the vegetation structure. The Mull flora contains more thermophillic elements such as *Camptodromites major* and *C. multinervatus* and *Amentotaxus*, while the Skye flora is composed almost entirely of Arcto-Tertiary elements. The differences in climate between these two floras and its potential effect on vegetation structure will be discussed in greater detail in section 7.6.5.2.

7.6.4 Palaeoclimate comparison between the Mull and Skye floras

As indicated in the previous section, the floras of Mull and those of Skye appear to be physiognomically different, which should be reflected in the climate signals they provide. Estimates of MAT from the two floras indicate that the Mull floras were growing in a warmer climate than those of Skye (Table 7.11, Figure 7.9). The Mull floras are consistently warmer than those of Skye for all three methods used in this study and the LMA derived estimates on average are 5.1°C warmer, for CLAMP 1 °C and for MLR 4.7 °C (Table 7.11, Figure 7.9).

The CLAMP estimates for both floras are similar with on average only 1 °C difference in MAT. The cause of this close comparability of MAT between the floras may be related to their shared angiosperm taxa. The Skye and Mull floras share six of the same angiosperm leaf types; these shared taxa also display the same physiognomic ranges. The physiognomy of the floras coupled with their low diversity could account for the comparable MAT estimates obtained from CLAMP.

Table 7.11. Mean annual temperature (°C) estimates from the mid Paleocene floras of Mull and Skye derived from LMA, CLAMP and MLR models.

	Mean annual temperature (°C)	
Physiognomic method	Mull	Skye
LMA1	8.8 ± 3.5	3.7 ± 2.4
LMA2	9.4 ± 3.3	4.6 ± 2.3
LMA3	7.0 ± 3.4	2.2 ± 2.3
LMA4	11.3 ± 4.2	5.2 ± 2.9
LMA5	8.4 ± 3.6	3.1 ± 2.5
LMA6	8.6 ± 3.4	3.7 ± 2.3
LMA7	7.9 ± 3.2	3.3 ± 2.2
CLAMP1	11.0 ± 1.7	10.3 ± 1.7
CLAMP2	12.5 ± 1.8	10.9 ± 1.8
CLAMP3	11.4 ± 1.1	11.1 ± 1.1
CLAMP4	13.0 ± 1.2	11.7 ± 1.2
MLR1	8.0 ± 2.0	3.4 ± 2.0
MLR2	5.2 ± 2.7	0.1 ± 2.3
MLR3	10.0 ± 2.0	5.5 ± 2.0

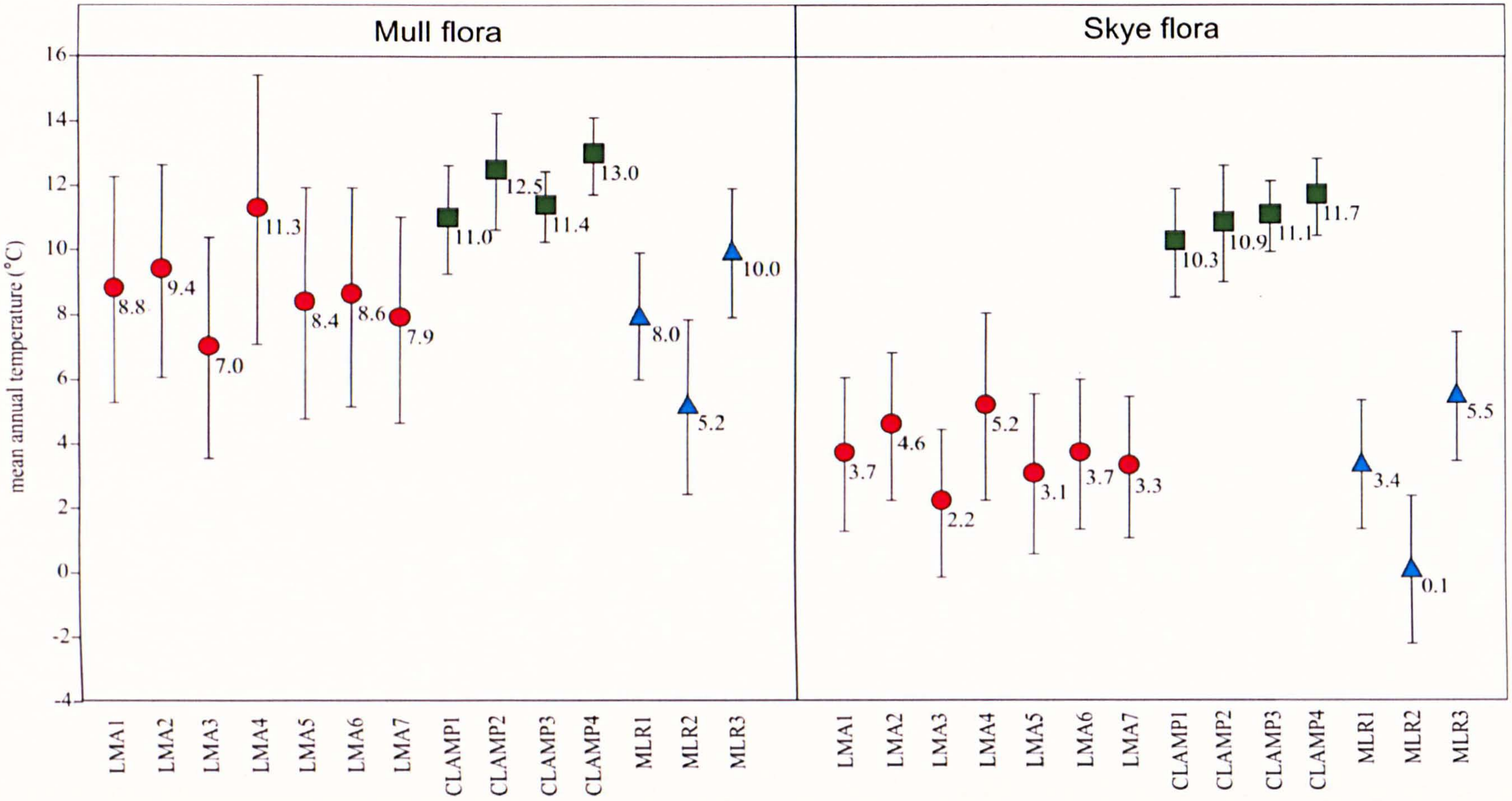

Figure 7.9. Mean annual temperature estimates derived from the mid Paleocene floras of Mull and Skye. Red Circles ● = LMA derived estimates, green squares 🟩 = CLAMP derived estimates, blue triangles = ▲ MLR derived estimates.

The margin percentage for the two floras is markedly different, the Skye flora has a margin percentage of 8.3% and Mull has a percentage of 25%. This difference in margin percentage is the primary factor for the difference in temperature estimates obtained from LMA and MLR. The estimates derived from these two methods are potentially more reliable as they are more strongly influenced by margin percentage, which is the most strongly correlated trait with MAT (Wolfe 1979, Wing and Greenwood 1993, Wilf 1997, Wiemann et al. 1998). The CLAMP estimates from both floras appear to be less influenced by margin percentage, which may suggest this method is a less reliable indicator of MAT for the BTVP floras or other Paleocene floras.

Estimates of seasonality (CMM and WMM) derived from the two floras indicate that the degree of seasonal temperature variation was different for the two floras. The climate estimates derived from the Skye floras indicate that the climate was more seasonal with greater range with colder CMM and cooler WMM estimates compared to those derived from Mull (Table 7.12, Figure 7.10). The CMM estimates for Skye are on average 0.9 °C cooler for CLAMP and 6.9 °C cooler than the MLR estimates derived from the Mull flora.

Similarly the estimates of WMM derived from the Skye floras are cooler compared to those of Mull, and are on average 1.2°C cooler for CLAMP and 3.6°C obtained from the MLR estimates. The degree of seasonality between the two floras appears to be relatively slight based on the CLAMP estimates, while those derived from the MLR models indicate the climate of Skye was considerably more seasonal compared to Mull.

As discussed in Chapter 6 and previously in this chapter, the estimates of CMM obtained from the MLR models may be unrealistically cold for both floras. This has important implications regarding the seasonality if the MLR estimates are unreliable. The low MAT estimates of the Skye flora are more suggestive of a cooler climate but if the WMM estimates are reliable for both methods the climate may have been indeed highly seasonal based on the MAT. If the WMMs are unreliable then the degree of seasonality may have been more comparable.

Table 7.12. Cold month mean temperature and warm mean month temperature estimates from the mid Paleocene floras of Mull and Skye derived from LMA, CLAMP and MLR models.

	Cold mean month temperature (°C)		Warm mean month temperature (°C)	
Physiognomic method	Mull	Skye	Mull	Skye
CLAMP1	0.3 ± 3.0	0.0 ± 3.0	22.0 ± 1.8	20.8 ± 1.8
CLAMP2	3.0 ± 2.6	1.6 ± 2.6	22.6 ± 1.8	20.8 ± 1.8
CLAMP3	0.9 ± 1.9	0.5 ± 1.9	22.6 ± 1.4	22.2 ± 1.4
CLAMP4	2.9 ± 1.9	1.6 ± 1.9	24.2 ± 1.6	22.8 ± 1.6
MLR1	-2.5 ± 2.6	-7.6 ± 3.6	23.9 ± 2.9	20.0 ± 2.9
MLR2	-5.9 ± 3.5	-14.8 ± 3.5	26.5 ± 2.5	23.3 ± 2.5

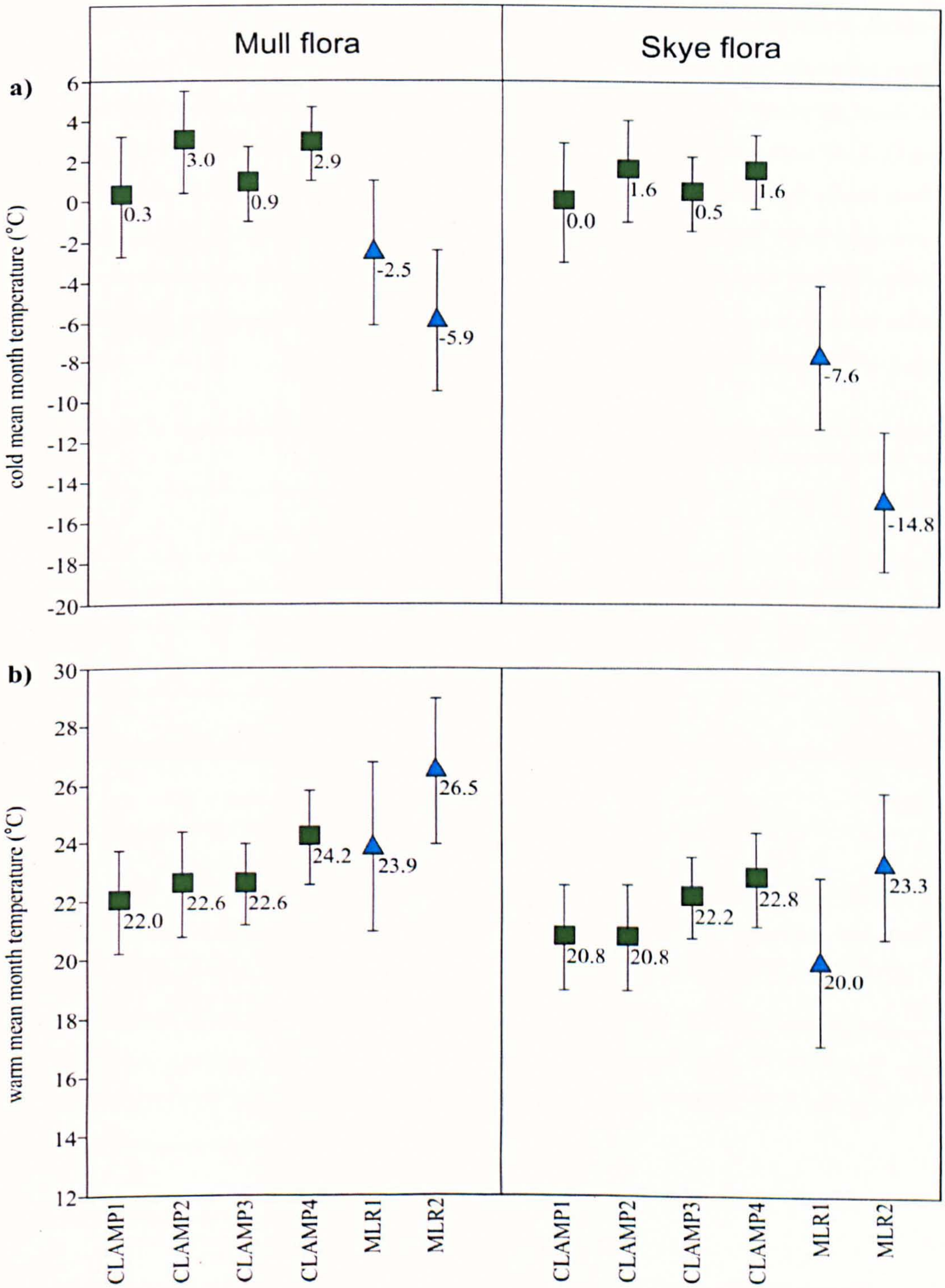

Figure 7.10. Seasonality estimates from the mid Paleocene floras of Mull and Skye, a) cold mean month temperatures, b) warm mean month temperatures.

Estimates of precipitation for both floras are relatively high and both are comparable with modern temperate rainforest conditions (Alaback 1991). The estimates of GSP derived from both floras are relatively comparable (Table 7.13, Figure 7.11). The estimates of GSP obtained from CLAMP analysis of the Mull flora (excluding CLAMP1 and CLAMP3) are on average 338mm higher than those of Skye. The estimates derived from the MLR models are however, on average 143mm higher for the Skye flora. As discussed previously in this chapter the accuracy of these estimates should be treated with caution. On this basis and on the close overlap between the estimates of both floras it is difficult to access if these two floras were subject to different levels of precipitation during the growing season.

Figure 7.11. Growing season precipitation estimates from the mid Paleocene floras of Mull and Skye derived from LMA, CLAMP and MLR models.

	Growing season precipitation (mm)	
Physiognomic method	Mull	Skye
CLAMP1	1525 ± 194	1380 ± 194
CLAMP2	2022 ± 317	1722 ± 317
CLAMP3	1550 ± 200	1409 ± 200
CLAMP4	2117 ± 331	1742 ± 331
MLR1	1263 ± 472	1795 ± 472
MLR2	1476 ± 300	1476 ± 300
MLR3	1809 ± 512	1705 ± 512

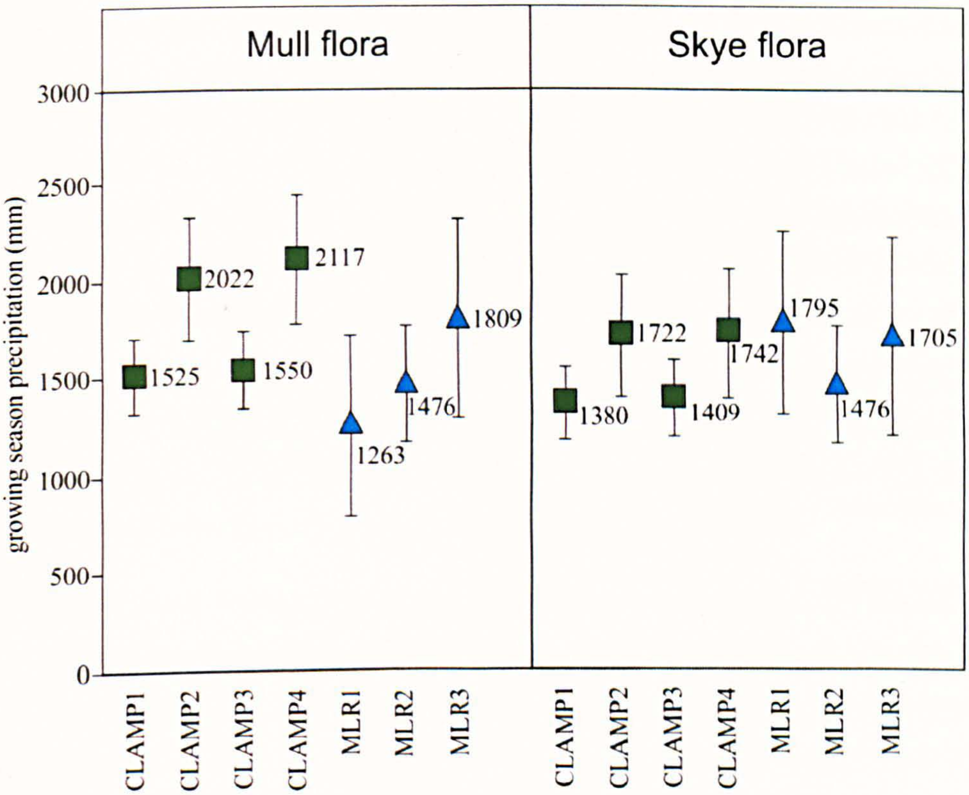

Figure 7.12. Estimates of growing season precipitation from the mid Paleocene floras of Mull and Skye.

7.6.5 Discussion of the climatic estimates

The results obtained in this study suggest the ambient climatic conditions changed during the time of the Mull and Skye floras. The Mull floras were growing in warm-temperate climate, while those of Skye were growing in a cool-temperate to temperate climate. This significant variation in temperature between the two floras cannot be explained by their difference in latitude as both localities were in their current configurations during the mid Paleocene (Ganerød et al. 2010). The difference in temperature must therefore be the result of climate change or differences in elevation.

7.6.5.1 Elevation and climate

The relative altitude of the two floras may represent a significant factor which could account for the disparate climate estimates. The cooler MAT estimates obtained from the Allt Mor flora of Skye floras could indicate that this flora grew at relatively higher altitude compared to those of Ardtun. This has been suggested by Jolley (1997) who interpreted the Allt Mor leaf beds as representing an upland taxodicaeous conifer forest, which grew at an approximate elevation of 1000m above sea level. The floras of Ardtun Mull could potentially represent a lowland setting as the lavas of the Staffa Formation of Mull display features which suggest that they were erupted in a subaqueous, possibly lowland environment (Kerr and Kent 1995).

As discussed in Chapter 6, section 6.4.4.3 the suggestion of an upland origin for the Allt Mor flora is questionable based on the relatively poor palynological record from this site. Indeed, the leaf record of Allt Mor is more indicative of Jolley's (1997) lowland swamp community in many respects, which could suggest a lowland setting. Leaf physiognomy has been used to determine palaeoaltitude (Wolfe 1993, Wolfe 1995, Wolfe and Spicer 1999), but has been shown to relatively unreliable with high standard error ± 2 km (Peppe et al. 2010). This high standard error would most likely mask the true altitudinal difference between the floras, and has not been considered a reliable method in this study. It is possible that the Allt Mor flora developed at a higher elevation compared to that of Ardtun but constraining this factor is difficult, and other factors such as climate change could equally account for the disparity of the temperature estimates of the floras.

7.6.5.2 Climate change

Climate cooling in the mid Paleocene could be a potential explanation for the observed temperature differences obtained from the floras of Mull and Skye. Evidence of mid Paleocene cooling in Western Europe has been observed in oxygen isotope records from bivalves from the North Sea (Buchardt 1977, Buchart 1978), Iberian reef communities (Baceta et al. 2005, Aguirre et al. 2007) and Foraminifera assemblages from the Atlantic (Haq et al. 1977). Climate cooling could account for the observed differences in the vegetation composition of the two floras. The cooling climate may have forced potentially thermophillic elements such as *Amentotaxus gladifolia* and *Camptodromites major* and *multinervatus* away from the BTVP. The conifer-dominated flora of Allt Mor Skye may indicate the vegetation changed from warm-temperate angiosperm-dominated vegetation to cooler temperate coniferous forest.

If climate cooling is responsible for the observed temperature differences between the two floras then the results obtained in this study indicate that cooling during in this interval may have been rapid and of high magnitude. Mean annual temperature estimates derived from LMA and MLR models from both floras indicate that climate may have cooled as much as 4.7 °C to 5.1 °C in 0.4 to 1 million years. The implications and causes of this cooling require further verification with other climate proxies from other areas in the Northern Hemisphere. These other proxies and the potential implications and causes of this mid Paleocene cooling event will be discussed in Chapter 8.

7.7 Summary

The fossil floras and sediments of Ardtun Mull have provided an interesting insight into the floral and palaeoenvironmental dynamics of other regions of the BTVP. The sediments in which the floras are preserved represent fluvial-lacustrine deposition, with periods of vegetation colonisation and succession. This flora contains a variety of plant types including liverworts, ferns, horsetails, *Ginkgo*, conifers and angiosperms.

Comparisons with lithology of the Ardtun leaf beds and the floras they contain indicate that possibly three community types are represented by the leaf assemblages. These include a disturbed riparian community associated with fluvial deposits, an angiosperm dominated marginal lacustrine flora, and a low diversity, open swamp community.

Climate estimates obtained from the physiognomy of the angiosperm fossils indicate that the climate was humid warm temperate and mildly seasonal. Controversy regarding the dating of this flora is partly resolved by the climate estimates obtained in this study, which are not indicative of the PETM but more comparable with cooler mid Paleocene, which is consistent with the radiometric dating.

Comparisons of the floristic composition of the Skye and Mull floras indicate that each shared similar vegetative components. The floras do appear to be distinct as each has taxa that are restricted to one site. The vegetation composition of the two floras is markedly different; the Skye flora represents a mixed coniferous forest, while the Mull flora is characterised as being angiosperm-dominated forest with minor conifer elements.

A comparison of the climate estimates obtained from both floras indicates that the climatic conditions in which these floras were growing was significantly different. The climate estimates obtained from the Mull flora are considerably warmer than those of Skye, which suggests abrupt climate cooling may have occurred in this region during the mid Paleocene.

Chapter 8: Discussion

8.1 Introduction

This chapter summarises results about the composition of the vegetation of the BTVP during the mid Paleocene and the climate record derived from these floras. The floras of the BTVP are then compared to coeval floras in the Arctic, Europe, North America and Asia to determine any similarities and differences between these floral provinces. The impacts of volcanism on the BTVP floras is discussed to determine the effects that volcanism may have had on floral development in this region and how it may have impacted floras more widely in the Northern Hemisphere. The palaeoclimate data from the floras of the BTVP are compared to other climate proxies, firstly to determine if the climate estimates obtained in this study are valid, and secondly to determine key trends in Paleocene climate change.

8.2 Paleocene floras of the Northern Hemisphere

Paleocene fossil floras have been recorded across the Northern Hemisphere including the Arctic, Europe, Asia and North America (Figure 8.1). The composition of these floras suggests that persistent floral zones existed at this time; these floral zones represent bands of vegetation that relate to specific climatic ranges. For example the vegetation of the high northern latitudes is called by some palaeobotanists the Arcto-Tertiary floral province or the broadleaved polar forest (Mai 1991, McIver and Basinger 1999, Collinson and Hooker 2003). The mid latitudes of the Northern Hemisphere appear to have contained a mixture of temperate and subtropical elements, and have been called mixed forest, subtropical forest or paratropical forest (Mai 1991, Mai 1995, Collinson and Hooker 2003, Kvacek 2010).

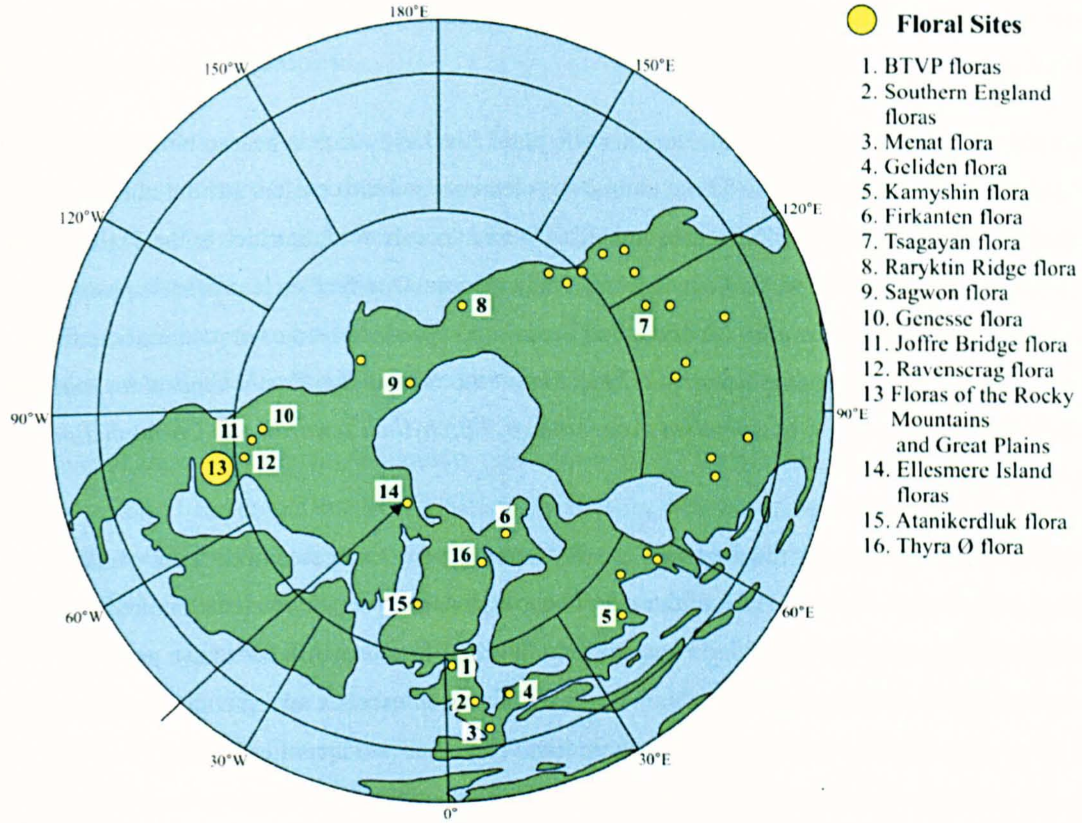

Figure 8.1. North Polar paleaeogeographic reconstruction of the mid Paleocene (59 Ma) showing the distribution of plant macrofossil site. Palaeogeographic reconstruction modified from Markwick (2007). Location of plant sites from Collinson and Hooker (2003).

This study of the fossil floras of the BTVP of the Isles of Skye and Mull has attempted to determine how these floras relate to those in the Northern Hemisphere during the Paleocene. In the following section the floras of the BTVP are compared to those of the Northern Hemisphere to establish which floras are most comparable, and to determine which floral zone or forest type the BTVP floras represent.

8.2.1 Paleocene floras of the BTVP

The floras of the BTVP provide the only macrofossil record of Paleocene terrestrial vegetation of northern Britain, and represent some of the oldest Paleogene floras of this region. In this study new collections of plant macrofossils were collected from three localities on Skye, Allt Geodh' a' Ghamhna, Allt Mor and Glen Osdale. The composition of these plant assemblages, plus the flora from Mull was compared with the known palynological record of Skye to determine the floral diversity and composition during the mid Paleocene.

Plant macrofossils and palynomorphs have also been recognised from other BTVP localities including the Small Isles (Rum, Canna, Eigg and Muck) and Northern Ireland (Boulter and Kvacek 1989, Jolley 1997). The combined floral evidence from this study and those of previous investigations indicates the floras of the BTVP were varied in their composition and structure, and were greatly influenced by topography, disturbance and volcanism (Boulter and Kvacek 1989, Jolley 1997, Jolley et al. 2009).

All BTVP localities share several characteristic plant families, which appear to be ubiquitous elements of this regional flora. These ubiquitous elements include conifers attributed to the families Cupresseaceae and Pinaceae, and angiosperms that show similarities to the Platanaceae, Cercidiphyllaceae, Betulaceae, Fagaceae and Juglandaceae. Conifers such as *Metasequoia*, *Glyptostrobus* and *Elatocladus* (*Sequoia* and *Taxodium*) appear to be the most common conifer taxa. The most common angiosperms include *Platanities hebridicus*, *Trochodendroides antiqua*, *Corylites hebridicus*, *Fagopsiphyllum groenlandica*, *Vitiphyllum sewardii* and *Cornophyllum hebridicum*.

These common taxa mask the degree of locality heterogeneity expressed in the sites of Skye, Mull and Northern Ireland. Each of these leaf bearing localities appears to have markedly different vegetation structures and compositions. The leaf fossils of Allt Mor have provided the most extensive record of plant fossils on Skye; this flora represents a mixed coniferous forest with riparian angiosperm-dominated communities. The other two localities on Skye, Allt Geodh' a' Ghamhna and Glen Osdale lack any conifer macrofossils and appear to represent disturbed low diversity angiosperm-dominated riparian vegetation.

The fossil floras preserved at Ardtun, Mull indicate that the vegetation was markedly different to that of Allt Mor on Skye. Conifer macrofossils, particularly members of the Cupressaceae, are rare components of the flora and angiosperms are the dominant element of the vegetation. Although both floras share similar ubiquitous types of angiosperms, the Ardtun flora includes angiosperm leaf types that are absent from the floras of Skye. These angiosperm leaf types currently have no clear affinity with modern families, but include forms such as *Camptodromites major* and *C. multinervatus*, whose physiognomy is more indicative of warmer climate conditions. The Ardtun flora also includes herbaceous plants including the sphenophyte *Equisetum* and the fern *Onoclea*, which have not been recognised in the leaf beds of Skye (see Chapter 7, Tables 7.9 and 7.10 for a comparison of floral components of Allt Mor, Skye and Ardtun, Mull).

The floras of Antrim are again different to other BTVP localities and include conifers attributed to the Pinaceae such as ?*Tsuga heerii* and *Pinus plutonis*, as well as poorly preserved Cupressoideae shoots and cones, attributed to *Cupressoconus machenryi*. Antrim angiosperms include forms that have not been reported in other BTVP localities and include *Ushia olafsenii*, *Platanites fraxinifolia*, *Macclinotockia dentata* and the monocot *Haemanthophyllum nordenskioldii* (Boulter and Kvacek 1989). The floras of Antrim in some respects are similar to the Allt Mor flora of Skye in terms of the their abundance of conifers, but differ in the composition of the angiosperms.

The leaf assemblages of Antrim, Mull and Skye show that these respective floras share a similar overall character, but display distinct local variations in vegetation composition and structure. This indicates that the vegetation cover of the BTVP was relatively heterogeneous, which may have arisen due to local differences in topography, palaeoenvironmental setting or climatic variation. This assertion is also indicated by the palynomorph record of the BTVP, which suggests several plant community types were present (Jolley 1997, Jolley et al. 2009).

In lowland areas several plant community types developed. Fluvial margins and floodplains appear to have been dominated by angiosperms and ferns, with taxodicaeous conifers growing in less disturbed proximal settings. Localised swamps in lowland areas supported a variety of taxodicaeous conifers and angiosperms such as members of the Juglandaceae as well as ferns. The upland or extrabasinal vegetation appears to be characterised by climax mixed coniferous forest, with stands of pines in the most upland setting (Boulter and Kvacek 1989, Jolley 1997, Jolley et al. 2009). This interpretation is supported by this study. The fossil floras of Allt Geodh' a' Ghamhna and Glen Osdale, Skye and Ardtun Mull represent more disturbed riparian angiosperm dominated communities and the flora of Allt Mor, Skye represents climax mixed-coniferous forest.

8.2.2 New discoveries from the BTVP

The fossil floras of Skye examined in this study represent the first attempts to identify these plant remains. Several plant taxa from the Allt Mor locality represent new species, which has significant bearing on the understanding of Paleogene vegetation as a whole.

The recognition of seven conifer species attributed to the Cupressaceae from the Allt Mor locality on Skye is of note. The presence of ovulate cones and shoots attributed to *Sequoia*, plus shoots and some ovulate cones attributed to Cupressoideae conifers such as *Chamaecyparis*, *Thuja, Mesocyparis* and *Calocedrus* indicates the BTVP provided an ideal setting for conifers in the Paleocene. The presence of *Sequoia* cones at Allt Mor indicates that this genus was present in the Paleocene of Europe. Additional collections of these cones are required and details of the shoot cuticles are required to confirm this assertion. At present cuticular preservation has not been observed for the *Sequoia*-like shoots from Allt Mor, but future collections may yield specimens with sufficient preservation for accurate diagnosis.

The presence of *Chamaecyparis* shoots with attached, albeit poorly preserved, ovulate cones may represent the earliest record of this genus. The current earliest unequivocal record of this genus is *Chamaecyparis eureka* from the mid Eocene of Axel Heiberg in the Canadian high

Arctic (Kotyk et al. 2003). If the Allt Mor species of *Chamaecyparis* is a true representative of this genus, it could extend the fossil record by more than 10 million years.

Paleogene conifer diversity in Europe is typically low (Kvacek 2010), which indicates that conifers were unable to gain a foothold in this region during this interval. The high abundance and diversity of conifers at Allt Mor is therefore surprising. Why conifers were able to thrive in Skye during the Paleocene and not elsewhere in Europe is still a mystery, but climate may be an important factor.

Members of the family Juglandaceae are a common element of the palynomorph assemblages of the BTVP (Jolley 1997, Jolley et al. 2009), which suggests that these plants were an important component of the BTVP vegetation. This family was beginning to diversify during the Paleocene, and both Europe and North America appear to have been important centres for diversification during this interval (Manchester 1987).

Three leaf morphotypes attributed to the Juglandaceae (AM 6-8) have been recorded from Allt Mor Skye. Morphotypes AM6 and AM7 are too incomplete to determine their generic affinity and have been assigned to the form genus *Juglandiphyllites*, and are perhaps comparable to the two species of Juglandaceae from Ardtun Mull (*Juglandiphyllites ardtunesis* and *Juglandiphyllites finlayii*). Morphotype 8, however, is the fourth most abundant angiosperm leaf type at Allt Mor and is represented by multiple, well preserved leaf specimens. This morphotype appears to most closely resemble the leaves of the modern genus *Platycarya*. This association with this modern genus is also partially confirmed by the pollen record, which indicates that *Platycarya*-like pollen producers were present on Skye and elsewhere in the BTVP during the Paleocene (Jolley 1997).

Currently no reproductive structures have been identified, which could confirm the presence of *Platycarya*, but if correct it could indicate that this genus may have appeared by the mid Paleocene with a European origin. If associated reproductive structures can be found in the plant-bearing sediments of the BTVP it would provide one of earliest records of a modern genus of the Juglandaceae. Future collection and suitable site selection is required to find these remains.

8.2.3 Paleocene floras of the Arctic and comparison with those of the BTVP

Paleocene Arctic floras have been recorded in Svalbard, Greenland, Canada, Alaska and eastern Asia. Arctic vegetation during the Paleocene was dominated by broadleaved deciduous angiosperms, deciduous conifers and herbaceous ferns and angiosperms (Mai 1991, Kvacek et al. 1994, McIver and Basinger 1999, Collinson 2002, Collinson and Hooker 2003, Herman et al. 2009). These floral sites, often referred to as the Arcto-Tertiary floral zone, are characterised by a selection of common taxa including the deciduous conifers *Metasequoia* and *Glyptostrobus*, a limited number of ferns such as *Osmunda*, *Onoclea* and *Coniopteris* and angiosperms attributed to the families Platanaceae, Cercidiphyllaceae, Betulaceae, Fagaceae, Juglandaceae, Hamamelidaceae and Trochodendraceae (Chaney 1950, Mai 1991, Kvacek et al. 1994, McIver and Basinger 1999, Collinson 2002, Collinson and Hooker 2003, LePage 2007). Paleocene Arctic floras from Svalbard, Greenland, Canada, Alaska and Asia are compared to the floras of the BTVP to establish if there are any similarities.

8.2.3.1 Paleocene floras of Svalbard

Early Paleogene plant assemblages are well known from Svalbard (Schweitzer 1980, Kvacek et al. 1994). The plant-bearing sediments of the Early Paleocene Firkanten Formation were interpreted by Schweitzer (1980) as having a coastal origin, with vegetation growing in costal bogs. These bogs supported a variety of conifers, most notably *Metasequoia* and *Taxodium*. In addition to these bogs, marginal and better drained environments supported mixed forests of *Sequoia*, *Ginkgo* and broadleaved deciduous angiosperms. The angiosperm taxa present in the Firkanten Formation include forms similar to those found in the BTVP including *Trochodendroides*-types, *Corylites hebridicus* and *Zizyphoides flabellum* (Schweitzer 1980, Kvacek et al. 1994).

In many respects this floral composition is similar to that of the BTVP, which may indicate close connectivity between these sites during the Paleocene. The high abundance of conifers and their taxonomic associations are broadly similar, as are the angiosperm leaf types. The high proportion of conifers within the Firkanten flora, including *Metasequoia*, *Taxodium* and *Sequoia* suggests that this flora is most similar to the Allt Mor flora of Skye. This is also indicated by the presence of *Zizyphoides flabellum*, which has been found at Allt Mor.

The Firkanten floras of Svalbard do, however, differ from those of the BTVP in that they lack representatives of some of the key families of the BTVP including the Juglandaceae, Vitaceae and Cornaceae. Their absence may be the result of the older age of the Firkanten flora, (age estimates 63 ± 2 Ma and 64 ± 2 Ma) (Blythe and Kleinspehn 1998), in that these plant taxa may not have evolved or spread into this region by the earliest Paleocene. Representatives of the Juglandaceae and Vitaceae, including form genera and species present in the BTVP, are present in the Eocene floras of Svalbard (Kvacek et al. 1994, Birkenmajer and Zastawniak 2005). This indicates that these plants types had colonised Svalbard in the later Paleocene or Early Eocene.

8.2.3.1 Floras of Greenland

The Atanikerdluk flora of north-western Greenland is the core flora of the Arcto-Tertiary floral zone (Mai 1991). This Early Paleocene flora is composed of a variety of broadleaved deciduous angiosperms, a minor broadleaved evergreen element, monocots, deciduous conifers and ferns (Koch 1963, Mai 1995). The Atanikerdluk flora is characterised by Koch (1963) as a *Macclintockia-Metasequoia-Cercidiphyllum* flora, which represents a climax forest state.

The Atanikerdluk flora contains elements such as *Metasequoia, Cercidiphyllum* (*Trochodendroides*), *Corylites* and *Fagopsiphyllum*, which are also common elements of the BTVP floras. The west Greenland flora also includes *Ginkgo* and *Cupuliferites* which are present in the Ardtun flora of Mull, and *Macclintockia* which occurs in Antrim, Northern Ireland.

Although similar to the BTVP flora the Atanikerdluk flora contains numerous elements that have not been observed in the leaf beds of the BTVP. The presence of several leaf types that may represent broadleaved evergreen types is a notable feature of the flora, which includes forms attributed to the Lauraceae, Magnoliaceae and Ericaceae (Koch 1963, Mai 1995). These plant types have not been recorded in the BTVP floras, which are dominated by deciduous leaf types.

The late Paleocene-Eocene Thyra Ø flora of northeast Greenland contains many Arcto-Tertiary elements such as *Metasequoia*, *Ginkgo*, *Elatocladus* and members of the Platanaceae, Cercidiphyllaceae and Betulaceae (Boyd 1990). This suggests that there is some similarity with the BTVP floras. The presence of *Musophyllum groenlandicum*, a possible banana relative, however, indicates that there are significant differences (Boyd 1992). Overall comparisons between the West and East Greenland floras and those of the BTVP suggest these floras shared some degree of connectivity during the Paleocene, but not all elements either migrated or survived in the BTVP.

8.2.3.3 Floras of the Canadian Arctic

Paleogene floras from Axel Heiberg and Ellsmere Island provide a wealth of information on high latitude vegetation of this interval, particularly forest structure and function in warm polar climates (e.g. Francis 1988, McIver and Basinger 1999, Kumagi et al. 1995, Williams et al. 2003a, Williams et al. 2003b, Williams et al. 2009). Leaf fossils from Ellsmere Island have in addition provided a record of Paleocene vegetation in the Canadian Arctic.

Floras from the Expedition Fiord and Strand Bay Formations of Ellsmere Island have been dated as Early and mid Paleocene respectively (McIver and Basinger 1999). The Expedition Fiord flora represents a low diversity assemblage of deciduous conifers and angiosperms, with aquatic vegetation. The sediments and leaf fossils represent fluvial deposition with local swamp development, represented by fossilised trunks of taxodiaceous conifers with diameters up to 3m (McIver and Basinger 1999).

The most abundant conifers of Expedition Fiord flora include *Metasequoia*, *Glyptostrobus*, and a possible evergreen taxodiaceous conifer may have been present. Pollen records also indicate that members of the Pinaceae may have grown at higher elevations, or at the margins of these floodplain habitats (McIver and Basinger 1999). The most abundant angiosperms include *Ushia* and several species of *Trochodendroides*, and at one locality leaves of *Corylites* and the possible liana *Archeampelos* (Vitaceae) were recovered along with other angiosperm taxa (McIver and Basinger 1999).

Floristically, the Expedition Fjord flora is similar to the BTVP with its abundance of deciduous conifers and angiosperms such as *Trochodendroides* and *Corylite*s. The presence of a possible liana from the family Vitaceae (*Archeampelos*), although distinct from *Vitiphyllum sewardii* of Allt Mor and Ardtun of the BTVP, indicates that the Canadian and Scottish floras may have had a similar ecology. The Expedition Fiord flora does differ to the BTVP in its lower diversity and apparent lack of members of the Platanaceae, Fagaceae and Juglandaceae.

The Juglandaceae are, however, represented by two species in the palynological record of the mid Paleocene Strand Bay Formation (McIver and Basinger 1999). Pinaceae pollen within the sediments of the Strand Bay Formation was suggested by McIver and Basinger (1999) to reflect extrabasinal upland pine forest. This interpretation is similar to the palynological record of the BTVP, and suggests that pine forests may have been a common feature of upland areas in the high and mid latitudes of the Northern Hemisphere during the Paleocene. The floras of Ellsmere Island therefore seem to be superficially similar to those of the BTVP, but differ in the low diversity of angiosperms.

8.2.3.4 Arctic floras of Asia and Alaska

Paleocene fossil floras from north eastern Russia and Alaska have provided an insight into Arctic vegetation of Asia and the links it had with North America during this interval. Early and mid Paleocene fossil floras have been studied from various localities in north eastern Russia and appear to share many characteristic plant taxa with coeval floras in Alaska (Herman et al. 2009).

Arctic Asian floras are typically of other Arcto-Tertiary localities in that they are dominated by broadleaved deciduous angiosperms, deciduous conifers and ferns (Akmetiev 2007, Herman et al. 2007a, 2007b, 2007c, Akmetiev and Beniamovski 2009, Herman et al. 2009). Important gymnosperm genera of Arctic Asia are broadly similar with those of the BTVP and include *Ginkgo*, *Metasequoia*, *Sequoia*, *Glyptostrobus* and *Mesocyparis*. Four important BTVP angiosperm form genera occur in Arctic Asian floral sites and include *Trochodendroides*, *Corylites*, *Juglandiphyllites* and *Zizyphoides* (Akmetiev 2007, Herman et al. 2007a, 2007b, 2007c, Akmetiev and Beniamovski 2009, Herman et al. 2009).

Paleocene floras of Amaam Lagoon area in far northeast Russia share many similarities with floras of Northern Alaska, which indicates that floral interchange occurred via Beringia (Herman et al. 2009). The Sagwon floras of northern Alaska span from the Early Paleocene to the mid Paleocene. This flora contains several BTVP taxa such as *Metasequoia*, *Trochodendroides* and *Corylites*, suggesting that the flora is similar to the BTVP. The Sagwon floras contain several angiosperm leaf types such as *Tiliaephyllum* and *Archeampelos*, which are absent from the BTVP (Herman et al. 2009).

The floral composition of Arctic Asian and Alaskan floras is similar to that of the BTVP providing further support for the widespread nature of these genera. The floras of Russia and Alaska do, however, differ to those of the BTVP in that they contain a wide variety of angiosperm leaf types that are absent from Scotland. These include form genera that are attributed to the families Platanaceae, Vitaceae, Cornaceae, Tiliaceae and Nyssaceae (Akmetiev 2007, Akmetiev and Beniamovski 2009, Herman et al. 2009).

8.2.4 Paleocene floras of Western Europe

Paleocene floras of Europe were perhaps the closest geographically to those of the BTVP, and therefore m share many floral similarities. Floral remains have been recovered from southern England, France and Belgium and have provided a record of mid to Late Paleocene vegetation in Europe (Mai 1995, Kvacek 2010), which can be used to establish any similarities with the BTVP floras.

8.2.4.1 Paleocene floras of France

The mid Paleocene floras of Menat, France have been dated as 60 to 61 Ma (Wappler et al. 2009) and are the closest in age to the BTVP floras than any other western European flora. The Menat flora is dominated by broadleaved angiosperm taxa, with rare conifer and fern components (Laurent 1912, Mai 1995). The angiosperm leaf types of Menat include several forms that are characteristic of the BTVP including members of the Platanaceae, Betulaceae and Juglandaceae (Laurent 1912, Mai 1995, Wappler et al. 2009, Kvacek 2010). The Menat flora includes the form genus *Corylites*, a characteristic BTVP taxon, but the platanaceous and juglandaceous elements are unlike those found in the BTVP.

Occurring with these temperate taxa are a host of thermophilic, possibly subtropical species attributed to the Fagaceae and Lauraceae (Laurent 1912, Mai 1995, Wappler et al. 2009, Kvacek 2010). The most striking difference between the Menat flora and the BTVP is their respective physiognomies. The Menat flora includes a wide variety of coriaceous leaf types that appear to represent thermophilic evergreen elements (Laurent 1912, Mai 1995). Coriaceous leaf types in the BTVP are relatively uncommon, only *Camptodromites major* and *C. multinervatus* present in the Ardtun flora are comparable with those Menat. This suggests that the Menat flora developed in warmer palaeoclimate that selected for evergreen coriaceous leaf types, compared to the cooler climates of the BTVP, which favoured deciduous leaf types.

The differences in physigonmy and taxonomy of the Menat flora indicates that it was quite unlike the flora of the BTVP, although their may have been some minor floral interchange as indicated by their shared taxa such as *Corylites* and *Glyptostrobus.* Overall the Menat flora appears to represent subtropical vegetation, which is distinct from the more temperate vegetation of the BTVP.

8.2.4.1 Paleocene floras of England

Similar floras to Menat occur in southern England at Herne Bay and Woolwich, and include types that are broadly similar to those found in the BTVP, including members of the Cercidiphyllaceae, Betulaceae and Juglandaceae (Crane 1981, Crane and Manchester 1982, Crane 1984, Mai 1995). The southern England floras also contain high proportions of thermophilic, possibly subtropical-tropical taxa (Mai 1995, Kvacek 2010). Late Paleocene floras from the Reading Beds in southern England again show this mix of temperate and subtropical taxa (Collinson 1983), which indicates that this flora although partially similar to those of the BTVP are distinct from this largely temperate vegetation type of the BTVP.

The Cobham lignite of southern England as mentioned in Chapter 7 (see section 7.3) represents vegetation growing prior to, and during the onset of the PETM (Collinson et al. 2009). The palynomorph assemblages of the Cobham lignite include forms similar to those found in the BTVP floras including members of the Juglandaceae (*Platycarya*) and members of the Cupressaceae (Collinson et al. 2009). Prior to onset of the PETM the vegetation of this area was dominated by ferns and woody angiosperm shrubs and trees, which developed in a fire-prone setting. At the onset of the PETM swampy conditions prevailed and supported taxodiaceous conifers and palms (Collinson et al. 2009). One of the most notable features of the Cobham lignite is the scarcity of pollen attributed to the Pinaceae; indeed only 10 bisaccate grains have been found. This is in contrast to the BTVP flora, which has a high proportion of Pinaceae pollen (Jolley 1997, Collinson et al. 2009). The Cobham lignite shares some taxa in common with the BTVP but was quite unlike the floras of the northern igneous province as it contains palms and a low abundance of pines.

8.2.4.2 Paleocene floras of Belgium

Late Paleocene floras from Belgium again show a mixed temperate and tropical character. The floras from Geliden, although in need of a reappraisal, show a similar aspect to other floras of the western Europe (Mai 1995, Akhmetiev and Beniamovski 2009, Kvacek 2010). The Geliden floras are dominated by angiosperms, the most important of which include several morphotypes of *Ushia* (Fagales) and *Dryophyllum* types (Fagaceae or Juglandaceae). Both of these leaf types occur in several European and Russian floras and are associated with warm climates (Akhmetiev and Beniamovski 2009, Kvacek 2010). *Ushia* has been reported from the BTVP floras of Northern Ireland, which suggests some floral connectivity (Boulter and Kvacek 1989). Palms have also been documented in this flora, which further indicates a warmer climate (Kvacek 2009, Fairon-Demaret et al. 2003).

A seed flora from the Dormaal Sand Member of Belgium is indicative of densely wooded landscape with numerous woody lianas (Fairon-Demaret and Smith 2002). The high proportion of woody lianas that bore fleshy fruits, their taxonomic association and the presence of crocodilians at this locality indicates a humid subtropical vegetation type (Fairon-Demaret and Smith 2002).

In-situ fossilised trees at the Tienen Formation in Belgium indicate that a swampy environment was dominated by monotypic stands of the conifer *Glytostrobus*. The presence of *Glyptostrobus* indicates some similarity with the BTVP floras, its presence in the Menat flora (Laurent 1912) indicates that it was one of the few conifers that were widespread in Europe during the Paleocene. The presence of *Sequoia* is indicated in Belgium by the presence of cone casts, but these have not been recently appraised (Fairon-Demaret et al. 2003). If these cones are indeed attributable to this genus then it may suggests that conifers present in the BTVP extended further south during the Paleocene.

8.2.5 Paleocene floras of Asia and North America

Paleocene fossil floras from Asia and North America have been extensively studied and have provided a wealth of information on the vegetation cover spatially and temporally. Comparisons are made in the following sections to determine how the floras of North America and Asia relate to the floras of the BTVP.

8.2.5.1 Paleocene floras of Asia

A distinct vegetation type persisted from the Maastrichtian through to the early Selandian (early mid-Paleocene) in Asia and eastern Europe. This vegetation type is often referred to as the Tsagayan ecotype and represents a temperate mesophilic flora characterised by ferns, *Ginkgo*, conifers and broadleaved angiosperms (Akhmetiev 2007).

Important fern taxa in the Tsagayan ecotype include *Onoclea* and *Osmunda*, which have similarities with the BTVP and Arctic floras such as Svalbard. Gymnosperms are a common component of this vegetation ecotype and include *Ginkgo* and members of the Cupressaceae, particularly taxodicaeous types. Broadleaved angiosperms are an integral component of the Tsagayan ecotype and include *Trochodendroides*-types and members of the families Cornaceae, Hamamelidaceae and Nyssaceae (Akhmetiev 2007).

The Tsagayan ecotype extended across Asia during the early Paleocene and has been reported in the Zeya-Bureya basin in south eastern Russia, areas around the lower, middle and upper Amur River, northeast China, Kamchatka Peninsula and Koryakia in Northeast Russia, northern Siberia, the Urals and Mongolia (Akhmetiev 2007, Akhmetiev and Beniamovski 2009).

The Tsagayan flora of Asia is compositionally similar to floras from the Arctic and the BTVP. Riparian components of the Tsagayan flora include *Ginkgo*, taxodicaeous conifers, *Trochodendroides*-types and members of the Platanaceae-Hamamelidaceae (Akhmetiev 2007). This riparian composition is similar to that found in BTVP localities such as Allt Mor Skye and Ardtun Mull, which suggests similar ecological relationships occurred over much of the Northern Hemisphere during the Paleocene.

The close similarity between the Tsagayan floras of Asia and the BTVP may indicate some degree of floral interchange took place in the early Paleocene. Floras from the Asia may have been able to reach the BTVP from two routes. The first route may have been overland via Europe or through Scandinavia and Svalbard. The presence of *Metasequoia* in the late Cretaceous Walbeck flora of Germany shows that Arcto-Tertiary elements were entering Europe during this interval (Kunzmann and Mai 2011). The migratory route taken by *Metasequoia* and other Arcto-Tertiary elements is currently unclear but may have been via Asia and the North Atlantic.

Significant changes in sea-level and vegetation composition occurred in the mid and late Paleocene in Asia. The development of two seaways had a significant impact on floral development in western Russia and Siberia in the Late Paleocene and Eocene. These seaways include the West Siberia epicontinental seaway that connected the Peri-Tethys with the Arctic Ocean and a latitudinal expanse of sea that connected the eastern Peri-Tethys with the Atlantic Ocean (through Europe) (Akhmetiev 2009). These seaways would have hindered floral interchange between Europe and Asia.

During the Selandian and Thanetian, floras similar to those of Geliden in Belgium (see section 8.3) occurred in Volga basin of southwestern Russia. These paratropical floras are typified by *Ushia*, *Chamaecyparis*, *Dewalquea*, *Macclintockia*, *Dryophyllum* and members of the Lauraceae (Mai 1995, Akhmetiev 2009). The Late Paleocene Kamyshin flora of the Volga Basin is a typical example of this Paratropical flora in Russia, which is similar to those found in western Europe during this interval. Similar paratropical floras occur throughout the mid latitudes of Russia and Kazakhstan, which indicates a persistent band of vegetation of this type extended over much of Europe and Asia during the mid to late Paleocene (Mai 1995).

As discussed in section 8.2.4, this paratropical flora type is significantly different to that of the BTVP floras. Despite similarities with Danian floras in Asia the mid and late Paleocene vegetation composition is markedly different to that of the BTVP. The cause of this shift in vegetation may be related to climate change. Why the floras of the BTVP retained a cooler climate flora, while similar aged floras in Asia changed dramatically from the temperate Tsagayan-type to subtropical/paratropical Geliden flora is currently unclear.

8.2.5.2 Paleocene floras of North America

Fossil floras from the Great Plains and Rocky Mountain region of the USA and Canada have provided excellent record that spans from the Late Cretaceous into the Eocene, and has arguably provided the most comprehensive record of Paleocene vegetation for the Northern Hemisphere. A detailed review of these floras is beyond the scope of this study, but comparisons will be made with those of the BTVP.

The Early Paleocene Paskapoo Formation of Saskatchewan and the Alberta Basin have provided an excellent record of vegetation from this region, which share many characteristic taxa with the BTVP floras. The Alberta Basin contains several floral localities most notably Genesse, Joffre Bridge and Munch's Hill (Chandrasekaram 1974, McIver and Basinger 1993, Hoffman and Stokey 1999, Hoffman 2002).

The early Danian Ravenscrag flora of Saskatchewan includes a highly characteristic BTVP genus, *Platanites* (Crane et al. 1988, McIver and Basinger 1993). The Ravenscrag *Platanites* is remarkably similar to the BTVP form, but it is several million years older, which suggests that this plant may have migrated from southern Canada, through Greenland and then into Scotland in the Early Paleocene. The Ravenscrag flora also includes numerous conifers such as *Elatocladus*, *Metasequoia* and *Mesocyparis*, all of which occur in the BTVP (McIver and Basinger 1993). These shared floral components, provide further evidence for floral connectivity and interchange between North America and Europe in the Paleocene. This flora does, however, differ to that of the BTVP as it lacks any members of the Betulaceae, and common components of the BTVP floras such as *Glyptostrobus* and *Ginkgo* are rare (McIver and Basinger 1993).

Floras from the Great Plains and Rocky Mountain region of the US contain a wealth of floras throughout the Paleocene. Of most direct interest for this study are the mid Paleocene (Tiffanian, North American land mammal age) floras. These floras show significant local variation, but are typically low in diversity compared to comparatively younger and older floras in this region (e.g. Hickey 1980, Wing et al. 1995, Gemmill and Johnson 1997, Peppe 2010). This low diversity is potentially mirrored in the BTVP floras, which show similar diversity curves to those in North America (Peppe 2010) (see Chapter 5, Figure 5.5). This may indicate that mid to high latitudes floras in the Northern Hemisphere were relatively species-poor during the mid Paleocene compared to the Early and Late Paleocene.

A detailed ecological study of a mid Paleocene flora from the Fort Union Formation, Wyoming has provided a useful insight into North American vegetation patterns in the mid Paleocene. The flora is relatively species poor with 28 morphotypes recognised, four of which are ecologically dominant (Gemmill and Johnson 1997). The dominant taxa include *Metasequoia*, *Corylites*, *Archeampelos* (a possible member of the Cercidiphyllaceae) and the aquatic herb *Fortuna* cf. This combination of taxa, with exception of the aquatic herb *Fortuna* cf. is very similar to that of the Allt Mor locality of Skye, suggesting similar forest types were widespread in the mid Paleocene.

Mid Paleocene floras of the Rocky Mountains and Great Plains are characteristic of polar vegetation with a high proportion of deciduous broadleaved angiosperms and conifers characteristic of higher latitudes and the BTVP (Manchester 1999, Collinson and Hooker 2003, Pigg and Devore 2010). Important taxa common to both the North America and the BTVP include gymnosperms such as *Metasequoia*, *Glyptostrobus*, *Mesocyapris* and *Ginkgo*. Angiosperms attributed to the families Platanaceae, Cercidiphyllaceae, Betulaceae, Fagaceae, Juglandaceae, Cornaceae and Trochodendraceae occur in both regions (Manchester 1999). Specific angiosperm leaf form genera that are characteristic of both regions include *Platanites*, *Cercidiphyllum*/*Trochodendroides*-types, *Fagopsiphyllum*, *Zizyphoides*, *Cornophyllum*/*Cornus* (Manchester 1999, Pigg and Devore 2010). Included in this list is the enigmatic seed *Calycites ardtunesis*, which occurs in North America and Ardtun, Mull (Manchester 1999).

Paleocene floras from North America do, however, differ to those of the BTVP in a number of aspects. This indicates that although floral interchange did occur, not all North America taxa entered Europe during the Paleocene. Important North American taxa not present in the BTVP include members of the Lauraceae, Zingiberaceae several genera within the Juglandaceae and Platanaceae and a variety of aquatic macrophytes (Manchester 1999). These taxa either represent North American endemics, or plants that have migrated from Asia, and have not subsequently migrated further eastward into Greenland and the BTVP (Manchester 1999). Why certain elements freely crossed from North America into Europe and vice-versa is unclear, but may be related to climatic tolerances and or competition with other taxa.

8.2.6 Summary of relationships of the BTVP floras with the Northern Hemisphere vegetation of the Paleocene

The floras of the BTVP appear to share many floral components with a broad spectrum of Northern Hemisphere floras of the Paleocene. Important BTVP elements such as *Onoclea*, *Ginkgo*, *Metasequoia*, *Glyptostrobus*, *Trochodendroides*, *Corylites*, *Zizyphoides* occur across the Northern Hemisphere. Other important BTVP taxa such as *Platanites* and *Fagopsiphyllum* had a more restricted distribution, and occur only in the Arctic and North America. Although a high proportion of the BTVP plant taxa occur in other geographical regions it does contain several taxa that appear to be endemic to northwest Britain during the Paleocene. These endemics include members of the Juglandaceae, and leaf types with unknown affinities from Ardtun Mull such as *Camptodromites* and *Davidoidea*.

A comparison with floras from other regions in the Northern Hemisphere has enabled a better understanding of how the floras of the BTVP fit within the vegetation scheme of the Paleocene. Floras preserved in western Europe are the closest spatially to the floras of the BTVP, and share some similar angiosperm taxa. The floras of Western Europe, are however, considerably different to those of the BTVP. Western European floras contain an abundance of thermophilic taxa, which indicate a warmer subtropical-paratropical climate state. The absence of these more tropical taxa in the BTVP indicates that the climate in this region was possibly too cool to support these plant types during the mid Paleocene. The floras of the BTVP contain an abundance and relatively high diversity of conifers. Conifers are a relatively minor component of western European floras, which may be due to warmer palaeoclimate in Europe the Paleocene. The cool humid climate of the BTVP may have been more favourable for conifers.

The recent review of the Paleogene forest types present in western Europe, the BTVP and the European Arctic by Kvacek (2010) indicates that warmer subtropical and paratropical forests were widespread across Europe during the Paleogene, but their upper limit may have extended only into the southern England. The boundary between the subtropical European flora and the warm-temperate to temperate flora of the BTVP would have been several degrees of latitude further south than the BTVP, possibly in central England during the Paleogene (Figure 8.2, 8.3).

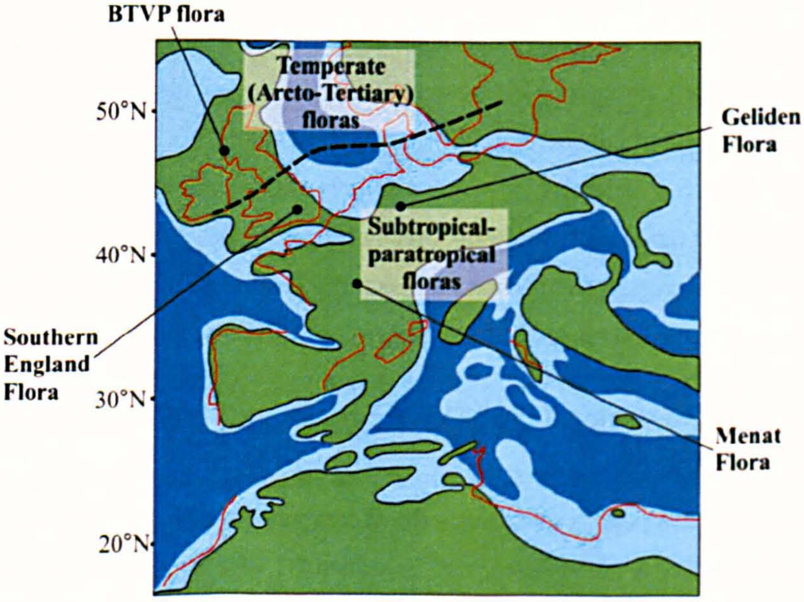

Figure 8.2. Palaeogeographic reconstruction of the early to mid Eocene of Europe showing the boundaries between temperate (Arcto-Tertiary) floras and subtropical-paratropic floras. Redrawn and modified from Kvacek (2010).

Early Paleocene floras in Asia are similar to those of the BTVP and both regions share many common Paleocene floral elements such as *Metasequoia*, *Glyptostrobus*, *Mesocyparis*, *Trochodendroides*, *Corylites*, *Cornus*/*Cornophyllum* and *Zizyphoides*. Floras of a similar age to those of the BTVP in Asia are, however, markedly different, and appear more similar to the subtropical and paratropical forests of Europe. Why Asian floras underwent a significant change at the time of the BTVP floras is unclear but it is probably linked to both marine transgression events and climate change during this interval.

North American floras indicate that vegetation in the Paleocene was broadly similar across the Northern Hemisphere as its composition is similar to Arctic, Asian and European floras. Mid Paleocene floras of southern Canada and the western interior of the US contain many BTVP taxa, most notably *Platanites* and *Fagopsiphyllum*. The North American floras like those of Asia do differ to those of the BTVP in number of aspects and contain many elements that have not been recorded in the BTVP or the Paleocene floras of Europe.

In overall terms of composition the floras of the BTVP appear to correspond most strongly with those of the Arctic, particularly floras from Svalbard, Greenland and Canadian Arctic. Important BTVP taxa such as *Metasequoia*, *Glyptostrobus*, *Trochodendroides*, *Corylites*, *Fagopsiphyllum*, *Cornophyllum* and *Zizyphoides* are widespread and in some cases ecologically important components of Arctic vegetation.

The BTVP flora is therefore regarded as a member of the Arcto-Tertiary floral zone based on its close similarities with vegetation of the Arctic Paleocene (Figure 8.3). Although similar to this cosmopolitan vegetation type, the BTVP differs from its counterparts in its high diversity of conifers (Allt Mor) and the high diversity, and early appearance of members of the Juglandaceae in both the leaf and pollen record.

Floristic interchange is indicated between the Arctic and the BTVP, which suggests vegetation was free to migrate across the volcanically active North Atlantic land bridge (Figure 8.3). This west to east migration may have started in the late Cretaceous or the early Paleocene, as floral elements that are highly characteristic of BTVP such as *Platanites* occur in southern Canada, which suggests that an earlier invasion of North American elements into the Arctic.

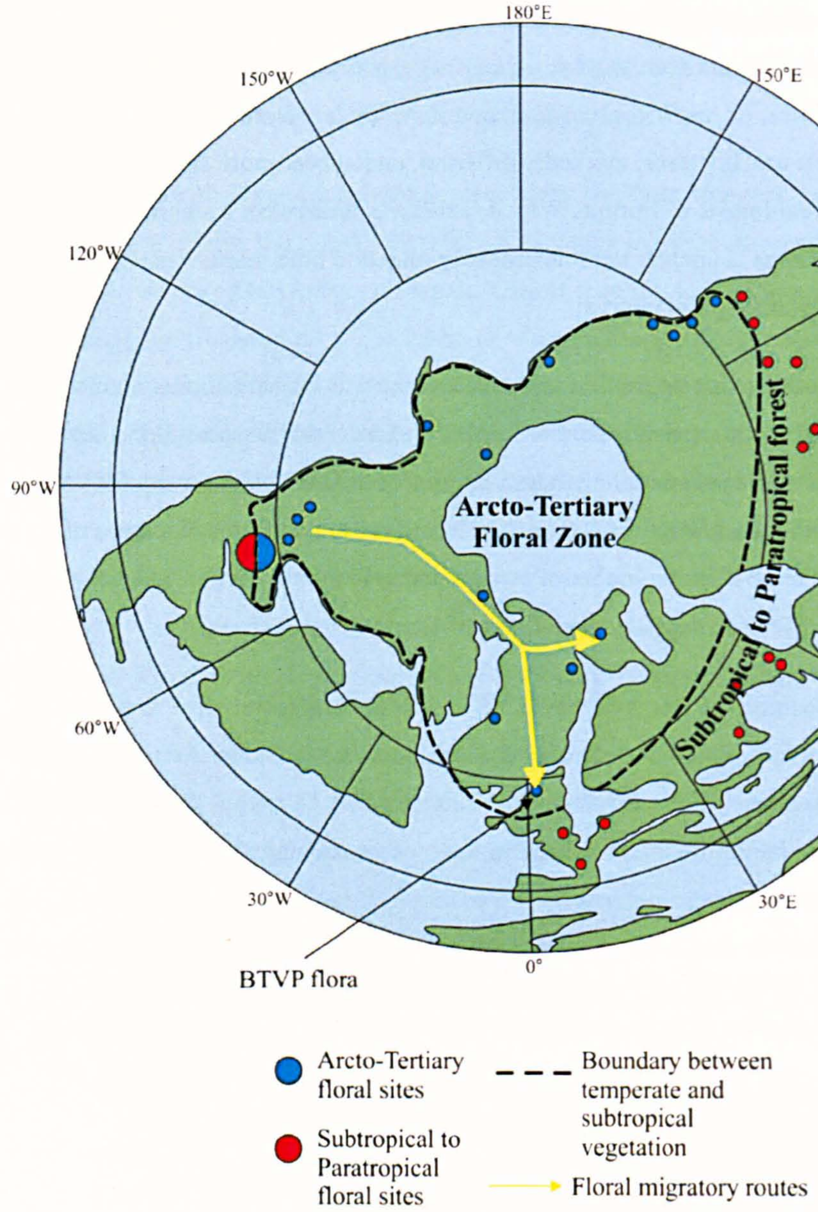

Figure 8.3. North polar palaeogeographic reconstruction of the mid Paleocene (59 Ma) showing floral provinces, macrofossil localities and migratory routes. Palaeogeographic reconstruction modified from Markwick (2007). Location of plant macrofossil sites from Collinson and Hooker (2003).

8.3 The effects of Volcanism on the BTVP floras

Volcanic environments are inherently hostile, as they impose numerous hazards and obstacles for organisms. Eruptive phases of volcanic environments can cause significant local, regional and global perturbations to the environment. These perturbations can be short-lived such as pyroclastic flows, or long term in the case of volcanic aerosols in the atmosphere. Areas of active volcanism pose serious challenges to colonising vegetation and ecosystem development.

Modern volcanic environments can provide an important insight into how the vegetation of the BTVP was able to initially colonise and develop in volcanic environments. The Hawaiian Islands provide an excellent opportunity to study how plant succession may operate on large igneous provinces. Hawaii is also an excellent analogue for the BTVP as the substrate and eruption style are broadly similar. The Hawaiian Islands, although similar in many aspects to the BTVP, are different, however, as the BTVP was not a volcanic island surrounded by ocean, but was connected to both Greenland and Europe. Extensive research has been carried out on ecosystem development and plant succession on these islands, which can be used as a guide to determine the nature of palaeo-plant succession and ecosystem development of the BTVP.

Plant succession on the Hawaiian Islands is influenced by numerous biotic and abiotic factors, such as substrate type, nutrient limitation, climate and altitude. The equable climate of the Hawaiian Islands provides excellent growing conditions for plants, enabling dense plant communities to develop on the volcanic substrates. Substantial variations in topography, substrate and its influence on the climate have produced a complex mosaic of environments on Hawaii (Raich et al. 1997). The diversity of these environments has enabled a variety of ecosystems to develop, each supporting distinct plant communities (Drake and Mueller-Dombois 1993, Raich et al. 1997). These studies can therefore provide a useful analogue to plant succession on the BTVP.

8.3.1 Colonisation of lavas

Plants that colonise lava flows have to be able to cope with low nutrients and desiccation, and in addition they require suitable dispersal mechanisms to reach recently formed lava flows (Raich et al. 1996). Among the first colonisers of the lava flows in Hawaii are bryophytes and lichens, as these plants are capable of growing directly on the lava surfaces (Aplet and Vitousek 1994). Ferns soon establish, but they are dependent on cracks and fissures in the lava surface for their development (Aplet and Vitousek 1994). The dominant tree on Hawaii, *Metrosideros polymorpha* is an excellent coloniser of lava flows and high densities of seedlings can develop on lava flows within two decades (Drake and Mueller-Dombois 1993).

This pattern of colonisation may have been similar for the BTVP with the earliest colonisers being bryophytes and ferns, which are an abundant component of the palynomorph record across the BTVP (Jolley 1997, Jolley et al. 2009). The abundance of some of the angiosperm leaf types (e.g. *Platanites hebridicus*, *Trochodendroides antiqua* and *Corylites hebridicus*) and their association with disturbed riparian environments indicates that these plants were capable colonisers. This colonisation ability in sedimentary environments may also have benefited their establishment in newly formed volcanic substrates and lava flows.

The ability of *Metrosideros polymorpha*'s ability to colonise Hawaii lava flows is related to its seed dispersal mechanism. These trees produce thousands of small seeds that are transported by the wind, which enables them to colonise distant sites. *M. polymorpha* also synchronises its seed dispersal to coincide with heavy rain during a nine week period between late November and late January, which enhances germination success (Drake, 1992). Colonisers of BTVP lava flows would therefore have to had suitable seed dispersal mechanisms to become established in the volcanic landscape.

The presence of mature forests along the margins of recent flows may act as refugia on Mt St Helens, as they are a source of seeds and colonists (Fuller and Moral 2003). Mature forest also provides a source of nutrients in the form of leaf litter and leached minerals from the soil. Leaf litter has been shown to increase the water holding capacity of the lava cracks, which further improves germination success and seedling establishment (Burton 1982, Drake, 1992, Raich et al. 1997). Seedling density of *M. polymorpha* on Hawaiian lava flows was shown to be greatest around the margins of the mature forest, which suggests that conditions around these margins provided more optimum conditions for seedling development (Drake 1992). Adjacent established forests may therefore provide both organic nutrients and increase the habitability of newly formed volcanic surfaces. This indicates that lava flows are colonised faster at their margins, and over time colonists advance into the centre of the flow.

Refugia in the BTVP may have played an important role in the colonisation of newly formed lava fields as they would have acted as islands of undisturbed forest within the newly formed flow or at their margins. These pockets of undisturbed forest would have provided nutrients in the form of leachates and leaf litter, as well as providing a source of colonists. Unlike Hawaii, which in many respects is closed system (little external recruitment of plant taxa), the BTVP would have bordered onto surrounding terrestrial areas in Northwest Britain and Greenland (Figure 8.4). Even during periods of intense volcanic activity where much of the vegetation of the BTVP was disturbed it could be later re-colonised by the relatively pristine forests surrounding the BTVP migrating into the lava fields.

8.3.1.2 Plant succession in volcanic environments

The study by Drake et al. (1993) has provided an excellent insight into plant succession and forest development in Hawaii over a period of tens to thousands of years. The first colonisers of the lavas in Hawaii include lihens and mosses, which are capable of developing on the lava surface shortly after its formation. These earliest colonist can colonise lavas rapidly, and have been observed on flows within a year of their formation (Drake 1992). Following these early colonists are ferns, which are capable of dispersing over large distances and reaching newly developed, barren lavas. These ferns are able to develop in the cracks in the lavas surface where nutrients and water accumulate (Drake 1992, Drake 1993).

After as little as two decades seedlings of the tree, *Metrosideros polymorpha* are able to establish on flows in montane Hawaii (Drake 1992). In Hawaii direct succession occurs, i.e. early pioneer taxa, in this case *Metrosideros polymorpha* also represent the dominant tree and climax vegetation type (Drake et al. 1993, Muller-Dombois 1992). The introduction of non-native species to islands has altered the succession patterns, however, and new climax communities are developing (Muller-Dombois 1992).

Within 400 years *Metrosideros polymorpha* dominated forest is able to develop on lava flows in montane rainforest zone in Hawaii (Drake et al. 1993). This rapid forest development in Hawaii is permitted by the equable climate, particularly the high rainfall of this region (Drake et al. 1993). It has been documented in even younger stands of 137 and 300 yrs that stem area of *Metrosideros polymorpha* has increased significantly from the early pioneer stands (Drake et al. 1993), which suggests that the overall productivity of the ecosystem is expanding even at this early stage.

In Hawaii forest stands of *Metrosideros polymorpha* begin to be outcompeted by tree ferns (*Cibotium* spp.), which reduce its ability to produce new cohorts of seedlings due to shading (Drake et al. 1993). Forests that have developed on 3000 year old flows appear to represent the climax forest type of humid montane parts of the Hawaiian Islands and are characterised by *Metrosideros-Cibotium* forest. These forests are multistratal and include an upper stratum of *Metrosideros polymorpha* canopy trees, a middle stratum of other pioneer tree species, and a lower stratum of tree ferns (Drake et al. 1993).

Plant succession in the BTVP may have had a similar pattern to that of the Hawaii, with a early colonisation phase followed by progressive seral stages until a climax community has established. A basic succession model has been produced for the BTVP floras to demonstrate the possible succession patterns that may have occurred in this region during the mid Paleocene (Figure 8.4). The first colonists of the lava flows like on Hawaii were likely to have been lichens, mosses and ferns (Figure 8.4). Following these plants would have been a wave of early pioneer species, capable of dispersing into the barren flows and adaptable enough to survive in the oligotrophic and potentially dry environment of the flows.

The first forests to develop on the lava flows of the BTVP were likely dominated by disturbance tolerant angiosperms (Figure 8.4). Common angiosperm elements of the BTVP are likely to have been the first pioneer shrubs and trees as they were probably capable of traversing the lava fields. Such angiosperm taxa may have included *Platanites*, *Trochodendroides*, *Corylites* and *Fagopsiphyllum*, but locally taxa such as "*Platycarya* cf." and *Camptodromites major* may have also been part of these early forest stands (Figure 8.4). These taxa may have formed stands, or thickets of woody shrubs and trees that at first would have been represented by a few hardy individuals and progressively would have formed closed canopy stands. Evidence on Hawaii indicates such forest stands can develop in as little as 400 yrs and it is possible such a rate of development may have been possible in the humid conditions of the BTVP (Figure 8.4).

The climax community of the BTVP would have been unlike that of the Hawaii as it is unlikely that it developed directly from pioneer species. Indeed pioneer species of the BTVP, ferns and angiosperm shrubs and trees may have been ousted and possibly marginalised by later succession angiosperms and climax conifer taxa due to shading and competition. In Hawaii a stable climax community is capable of developing in less than 3000 years. It is difficult to determine the length of time required for climax forest to develop on in the BTVP. But based on the rapid formation of the lava fields and the wide spread occurrence of suspected climax forest species in the pollen record (Jolley 1997) it is likely that climax communities may have been able to develop in as little as 3000 to 5000 years (Figure 8.4).

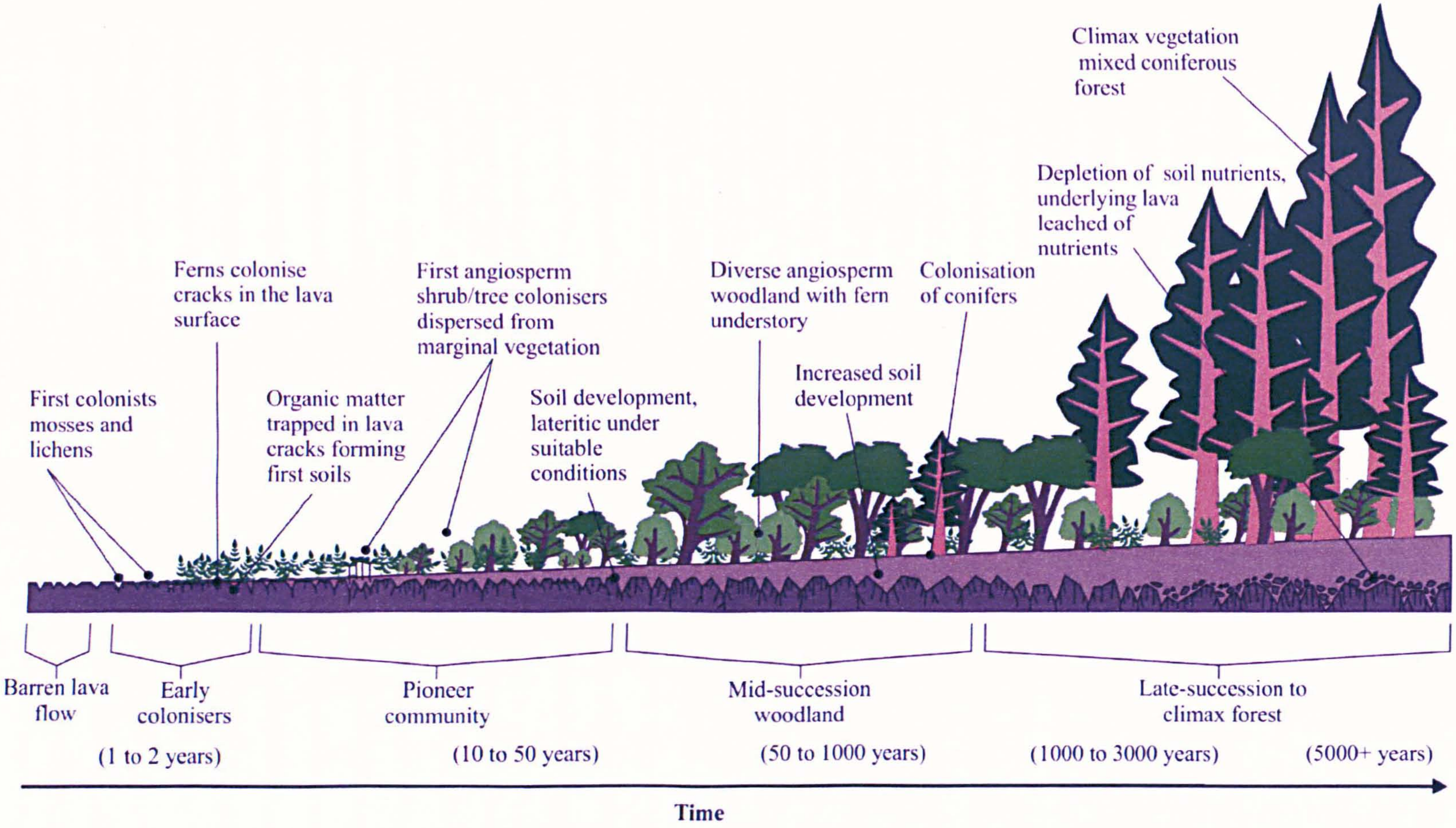

Figure 8.4. Generalised plant succession transect showing the proposed stages of vegetation succession on the lava flows of the BTVP. Image not to scale.
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8.3.1.3 Nutrient limitation

An important factor for the development of ecosystems on lava flows is nutrient limitation because newly formed or young lavas tend to provide little vital nutrients such as nitrogen and phosphorous (Raich et al. 1996). Plant communities that developed on the lavas of the BTVP would have had to cope with these low nutrient conditions. Studies on modern vegetation and soil nutrients on Hawaii may provide some insight into how the Paleocene vegetation of the BTVP was able to establish.

Young volcanic sites are impoverished in nitrogen and phosphorous (Raich et al. 1996). Weathering of volcanic the substrates and tephra introduces vital nutrients and cations for plants, particularly phosphorous. Phosphorus is essential for plant growth, and in most tropical forests it is impoverished (Vitousek 1984). Young volcanic sites in Hawaii are phosphorous-limited, as insufficient weathering and erosion of the volcanic substrate has not yet taken place (Raich et al. 1996). As the minerals in the lava and ash decompose through weathering they can provide a major source of nutrients for vegetation, but these sources become impoverished after ~100 000 years (Vitousek 2004).

Nitrogen is another key element for plant growth and it too is limited in young volcanic sites. Its low concentration therefore hinders plant growth in the early stages of ecosystem development (Vitousek et al. 1993). Nitrogen can be incorporated into the system through external sources, such as nitrogen-fixing lichen and bryophytes (Matzek and Vitousek 2003), and precipitated by cloud water (Heath and Hubert 1998). However, nitrogen inputs from both these sources are greatest when forest density and canopy cover are high (Heath and Hubert 1998, Matzek and Vitousek 2003). Younger sites with limited canopy cover are less likely to receive inputs of nitrogen from these sources, and so nitrogen accumulation is slowed, while older flows with more mature forest can obtain nitrogen from these sources.

Volcanic eruptions can provide an important source of both phosphorous and nitrogen through degassing and thermal interaction between hot lavas and the atmosphere. Volcanic degassing on Hawaii has been shown to provide a source of plant accessible phosphorous in the form of phosphorous pentoxide (P_4O_{10}) (Yamagata et al. 1991). The eruption of hot lavas can also provide a source of nitrogen to ecosystems, as the high temperatures of the lavas facilitates the fixing of plant accessible nitrate (NO_3) from the atmosphere (Heath and Heubert 1999, Heubert et al. 1999, Mather et al. 2004). Volcanic fog (vog) produced from eruptions has been shown to contain several orders of magnitude greater amounts of nitrate compared to normal background levels (Heubert et al. 1999). Plant accessible nitrogen from volcanic sources is then deposited from the atmosphere where it can provide a vital source of nutrients to oligotrophic volcanic ecosystems (Heath and Heubert 1999).

It is probable that recently colonised lava flows in the BTVP would have been nutrient poor, thus reducing the potential for colonisation and development of early pioneer communities. The humid climate of the BTVP may have facilitated the weathering of the lava surfaces and ash deposits, which may have provided a vital source of phosphorous to the burgeoning plant communities. The large scale of the volcanic eruptions in the BTVP may have provided a significant source of nitrate through thermal fixation, and degassing of plant accessible phosphorous may have provided an additional source of nutrition to BTVP vegetation. The BTVP floras in their early stages of development may therefore have been dependent on allochthonous sources of nutrients for their development.

An investigation by Jolley et al. (2008) on the nutrient dynamics and plant communities of the Miocene Columbia River Basalt, United States has provided an important insight into the nutrient and floral dynamics of Continental Flood Basalts (CFBs). The findings of Jolley et al. (2008) show that volcanically derived sources of nitrogen and phosphorous were vital for floral development at the Columbia River CFB.

The proximity to eruption centres was shown to have a profound impact on vegetation patterns at Columbia River. Sedimentary sequences most proximal to eruption centres indicate that possible eutrophic conditions developed, with high algal and diatom abundances. Vegetation that was growing more distally appears to have received less volcanically derived nutrients (Jolley et al. 2008). These communities were highly variable, some appear to be dominated by nitrogen fixing species, which were capable of improving soil nitrogen independent of volcanism. A second community type that lacks these nitrogen fixers, may have received nutrition from the weathering of volcanic ash (Jolley et al. 2008).

These findings indicate that nutrient levels in CFBs would have been highly variably spatially. The floras of the BTVP developing on lava surfaces may have received varying levels of volcanically derived nutrients depending on their proximity to eruption centres and whether volcanic ash was present.

Over time nutrient dynamics on lava flows and the ecosystems they support changes. On Hawaii flows that are between 2000-5000 years old tend to have better developed soils with higher organic matter content, with higher plant-accessible nitrogen and phosphorus concentrations compared to younger flows (Raich et al 1997). Sites of this age range offer optimum conditions for plant growth and ecosystem development, but they are still nutrient impoverished compared to other tropical forests (Raich et al 1997).

Soils on lava flows that are 5000 years old show a substantial decline in nutrient concentration and primary production, which indicates that these volcanic soils become exhausted relatively rapidly (Kitayama et al 1997). Modelling of long-term ecosystem development on Hawaii showed that ecosystem stability was never reached and allochthonous sources of nutrients were still required even after a period of 20,000 years (Raich et al 2000). This suggests that weathering of volcanic rock/ash and other allochthonous inputs are necessary for the long term development of volcanic ecosystems on Hawaii.

Under the assumption that similar patterns of nutrient accumulation and subsequent depletion occurred in the BTVP as in Hawaii it may indicate that the plant communities of this volcanic province underwent three phases of development. The first stage was the initial colonisation of the lava flows on nutrient-poor soils. The second stage was a period where soil organic matter and nutrients were high and relatively stable, and thus supported a diverse plant community. The final stage was a developed, but oligotrophic community, where soil nutrients had become exhausted due to prolonged leaching (Figure 8.4). All of these communities would likely be dependent on allochthonous sources of nutrients for their continued development.

8.3.1.4 The role of volcanic disturbance on BTVP vegetation

Ecosystems developing on volcanic substrates not only have to contend with possible desiccation and nutrient limitation but also have to be able to cope with disturbances inherent to volcanism. Such disturbance include the development of new lava flows, which can rapidly destroy standing vegetation, and the wildfires that may spread from these eruptions can cause disturbance over wider areas than the flow (Del Moral and Grishin 1999) (Figure 8.5). Volcanic ejecta ranging from fine volcanic ash to pyroclastic material can either enhance ecosystem function by providing vital nutrients, or can severely devastate plant communities (Del Moral and Grishin 1999). Volcanic degassing can have a significant impact not just on local but on global scales, as large volumes of gases, principally CO_2 and SO_2 (sulphur dioxide) can be emitted from volcanic eruptions (Siggurdsson 1990).

The lava sequences of the BTVP indicate that high volume eruptions were formed in relatively short intervals of one to two million years (see Chapter 2 section 2.3). Individual flows would have covered tens of square kilometres and would have devastated standing vegetation (Figure 8.5). The development of the BTVP lava sequences would have been perhaps the most important disturbance mechanism to BTVP vegetation. The effects lava flows had on BTVP vegetation is elegantly displayed at McCulloch's Tree on Mull, where lava flows had spread into a swampy environment and destroyed, and entombed the standing vegetation.

Palynomorph assemblages found throughout the lava sequences of the BTVP suggest that although lavas may have greatly affected vegetation it did not decimate it entirely. The widespread occurrence of presumed climax taxa (taxodiaceous and pinaceous pollen) indicates that BTVP vegetation was resilient to volcanic disturbance and was able to re-colonise and develop into climax communities relatively rapidly after periods of volcanism.

The outer margins of the BTVP would have contained relatively pristine vegetation which could disperse into the BTVP during quiescent phases. The pre-Paleogene landscape with its diverse topography may have also provided refugia from the eruptions (Figure 8.5). Pockets of undisturbed forest within the lava fields would have provided a source of colonists to newly developed, barren lava flows and permitted the establishment of communities more rapidly. Fluvial systems may have also provided corridors for vegetation to colonise newly developed flows. The sedimentary environments produced by deposition of sediments in rivers and lakes may have provided a more hospitable environment for BTVP vegetation compared to the lava flows. The sedimentary record on Skye and Mull indicates that rivers developed on the lava surface (Williamson and Bell 1994, Kerr and Kent 1995), these fluvial environments may have therefore provided an important source of vegetation to the surrounding lava flows (Figure 8.5). Although the lavas may have devastated the standing vegetation it appears from the vegetation record that plants were able to cope with the frequent large scale eruptions, possibly because of these refugia.

Wild fires that resulted from the lava flows could have the potential to cause significant disturbance to vegetation. The presence of subangular equidimentional black wood in palynological samples, particularly in the Palagonite Tuff plant beds of northern and eastern Skye indicates that wild fires may have been frequent (Jolley 1997). Fire may well have affected the successional scheme of the BTVP vegetation by removing dominant species and enabling more disturbance tolerant species to re-establish (Figure 8.5). The humid conditions of the BTVP may have partially mitigated the intensity of these fires, however, and reduced widespread disturbance to BTVP vegetation.

The presence of pyroclastic and tuff deposits indicate that more explosive volcanism occurred in the BTVP. Pyroclastic flows would have devastated local vegetation, much like recent pyroclastic events have had on Mt St. Helens (Fuller and Moral 2003). A high proportion of the pyroclastic deposits recognised in the BTVP have, however, been subsequently reinterpreted as mass movement deposits (see Brown et al. 2009). This suggests that these events may have been rare and perhaps restricted to sites near to central volcanoes (Emeleus and Bell 2005, Brown et al. 2009, Holohan et al. 2009). It is likely therefore that pyroclastic flows had a limited effect on BTVP vegetation as a whole, but may have been locally highly destructive to vegetation growing close to central volcanoes.

Tuff deposits, however, are much more widespread and are common feature of interbeds across the BTVP, but are typically not extensive and generally are < 1m thick (Emeleus et al. 1996). The structure and composition of the crystals within these tuff deposits suggests they were deposited sub-aerially and may have a pyroclastic origin. The crystals and lithic fragments within these tuff deposits often differ significantly to the surrounding lava flows and are more indicative of evolved magma types and explosive volcanism (Emeleus et al. 1996).

A high proportion of the tuffaceous deposits appear to represent short intervals, as their overall structure indicates that only low levels of weathering occurred prior to their entrapment by later flows (Emeleus et al. 1996). It is likely therefore that these tuff deposits may mark periods of reactivation of volcanism following quiescent phases where more evolved magmas were erupted with the more basic effusive lavas. The combination of large scale effusive eruptions and localised explosive volcanism may have been a significant source of disturbance to BTVP vegetation.

Volcanic gas emissions, particularly sulphate aerosols can have a significant impact on vegetation by causing severe damage to leaf tissues, which can result in major vegetation mortality events (e.g. Winner and Mooney 1980, Grattan and Pyatt 1994, Delmelle et al. 2002). Leaf tissues often display signs of damage caused by volcanic gas emissions such as darkening of the tissue or necrosis (e.g. Winner and Mooney 1980, Delmelle et al. 2002). Fossil leaves may therefore record the effects of volcanic gases on vegetation. These features have, however, not been recognised on the BTVP leaves. This perhaps is partly due to limited preservation of mesophyll tissue and damaged leaves may also degrade more rapidly in sedimentary environments and therefore have less preservation potential (Ferguson 1985). Although no direct evidence for damage caused by volcanic gas emission has been observed it is likely that volcanic degassing would have had a significant impact on vegetation of the BTVP.

The scale of volcanic disturbance caused by BTVP volcanism would have varied significantly depending on the intensity and relative duration of the disturbance mechanisms. Lava flows would have had a more localised effect on vegetation, but the intensity of disturbance may have been severe resulting in complete destruction of established communities. Wild fires caused by the interaction of the hot lavas with vegetation may have extended the disturbance radius of the lava flows, as the fires may have been able to spread over larger spatial scales. The ejection of tuff from eruptions could have had the potential of effecting vegetation across the BTVP, because of its ability to be transported and subsequently deposited over large spatial scales. Volcanic degassing may have also introduced another source of disturbance, which could have severally damaged and killed standing vegetation. The vegetation record of the BTVP indicates that despite of these sources of disturbance plant communities were able to survive or re-establish themselves after periods of volcanism.

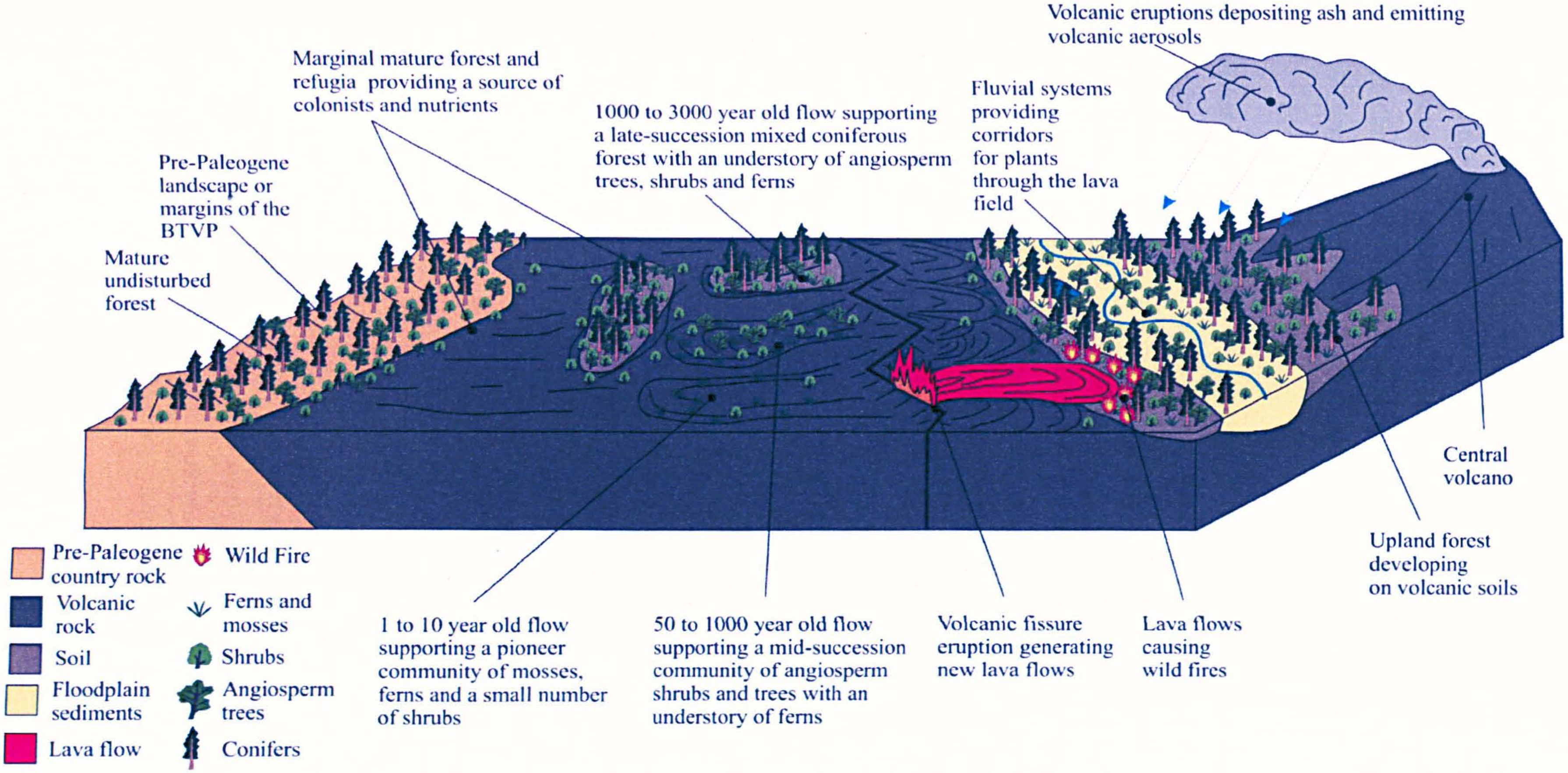

Figure 8.5. Generalised schematic diagram of the BTVP, showing the impacts of volcanism on the vegetation and plant succession patterns on the lava fields.

8.3.2 Summary

Modern volcanic environments, particularly the Hawaiian Islands have provided an important insight into how the volcanic environment of the BTVP may have affected the vegetation. The development of the extensive lava fields of the BTVP would have presented a significant challenge for vegetation entering this region. The vegetation of the BTVP would have had to cope with low nutrients and disturbance caused by volcanism. The fossil floral record indicates that despite of these obstacles plants were able thrive in the BTVP, and recover after disturbance.

Plant succession patterns on Hawaii have provided an insight into how BTVP succession may have developed on the lava flows. Lichens, mosses and ferns were likely the first colonists. These would have been followed by woody angiosperm shrubs and trees, which were capable of colonising and surviving on the immature flows. Progressive increases of nitrogen and phosphorous through weathering of the volcanic substrate coupled with addition nutrients from external sources would have facilitated the establishment of late succession angiosperm dominated woodland. This woodland would have then been succeeded by mixed coniferous forests, which is suggested here as the climax community type for the BTVP.

Disturbance caused by NAIP volcanism would have played a vital role in the shaping of the plant communities. Lava flows, wildfire, explosive volcanism and volcanic degassing may have contributed to the disturbance of plant communities. Despite of these potential disturbance mechanisms it is apparent from the floral record that vegetation of the BTVP was able to survive and indeed flourish in this volcanic environment. The margins of the BTVP and refugia within it would have provided a source of colonists and nutrients to the volcanic landscape during quiescent phases.

8.4 Paleocene climate records

8.4.1 Introduction

The palaeoclimate estimates derived from the angiosperm leaf morphotypes of Allt Mor, Skye and Ardtun, Mull have provided an insight into mid Paleocene climates. To test the reliability of these results they must be compared to other independent climate proxies from the Northern Hemisphere. The marine isotopic record, the terrestrial botanical record, atmospheric CO_2 levels and other climate proxies are compared with those obtained from the BTVP floras. Firstly this will help establish if the results from this study are valid, and will secondly provide information on how these results fit within the global climate record of the Paleocene.

8.4.2 Isotopic record of Paleocene climate

The Paleocene was warm with benthic marine temperatures ranging from 6 °C to 12 °C, and low latitudinal temperature gradients (Zachos et al. 2001). The general climate trend through the Paleocene was a decrease in marine temperatures during the Early and mid Paleocene (Danian to Selandian) followed by progressive warming in the Late Paleocene (Thanetian), which culminated in by pronounced warming at the end of the Paleocene with the Paleocene/Eocene Thermal Maximum (PETM) (Zachos et al. 2001, Zachos et al. 2008, Westerhold et al. 2011) (Figure 8.6).

The high resolution Paleocene benthic isotopic record produced by Westerhold et al. (2011) (Figure 8.6) has provided an excellent basis to access climatic change during this interval, and to establish how the climate data obtained from floras of the BTVP relate to the oceanic record. The focus of this discussion is on the mid Paleocene climate record and events prior and proceeding this interval (~62 to 59 Ma), as this is most relevant to floras of the BTVP.

The oxygen isotope record indicates that a period of relative cooling in the benthos began at ~63 Ma and continued throughout much of the Danian and Selandian until 59 Ma, with the greatest phase of cooling between ~61 to 59 Ma (Zachos et al. 2001, Westerhold et al. 2011). The positive oxygen excursion during this interval indicates benthic marine temperatures declined by ~3 °C from 63 to 59 Ma. This cooling in the oceans is consistent with cooling trend for the BTVP floras.

The isotopic record does, however, indicate a warming event occurred at 61.75 Ma, and when marine temperatures increased rapidly by 2 °C (Westerhold et al. 2008, Westerhold et al. 2011). This warming event is termed the Late Danian Event (LDE) (Figure 8.6), and is marked by a negative $\delta^{13}C$ and $\delta^{18}O$ values (Westerhold et al. 2011).

The extensive laterite sequences of Interbasaltic Formation of Antrim, Northern Ireland may potentially correspond to the LDE. The interbasaltic formation has been dated as 61.3 ± 0.3 Ma (Ganerød et al. 2010), which would suggest it is younger than the LDE. This age is based on an intrusive feature, the Tardee Rhyolite that is younger than much of the laterite sequences. It is possible therefore that development of the extensive laterites of the Interbasaltic Formation coincide with the LDE, and their formation was facilitated by the enhanced warmth of the LDE. The absence of such extensive laterites elsewhere in the BTVP supports this assertion that the Antrim laterites formed under warmer, possibly subtropical conditions compared to the more temperate conditions later in the BTVP's development.

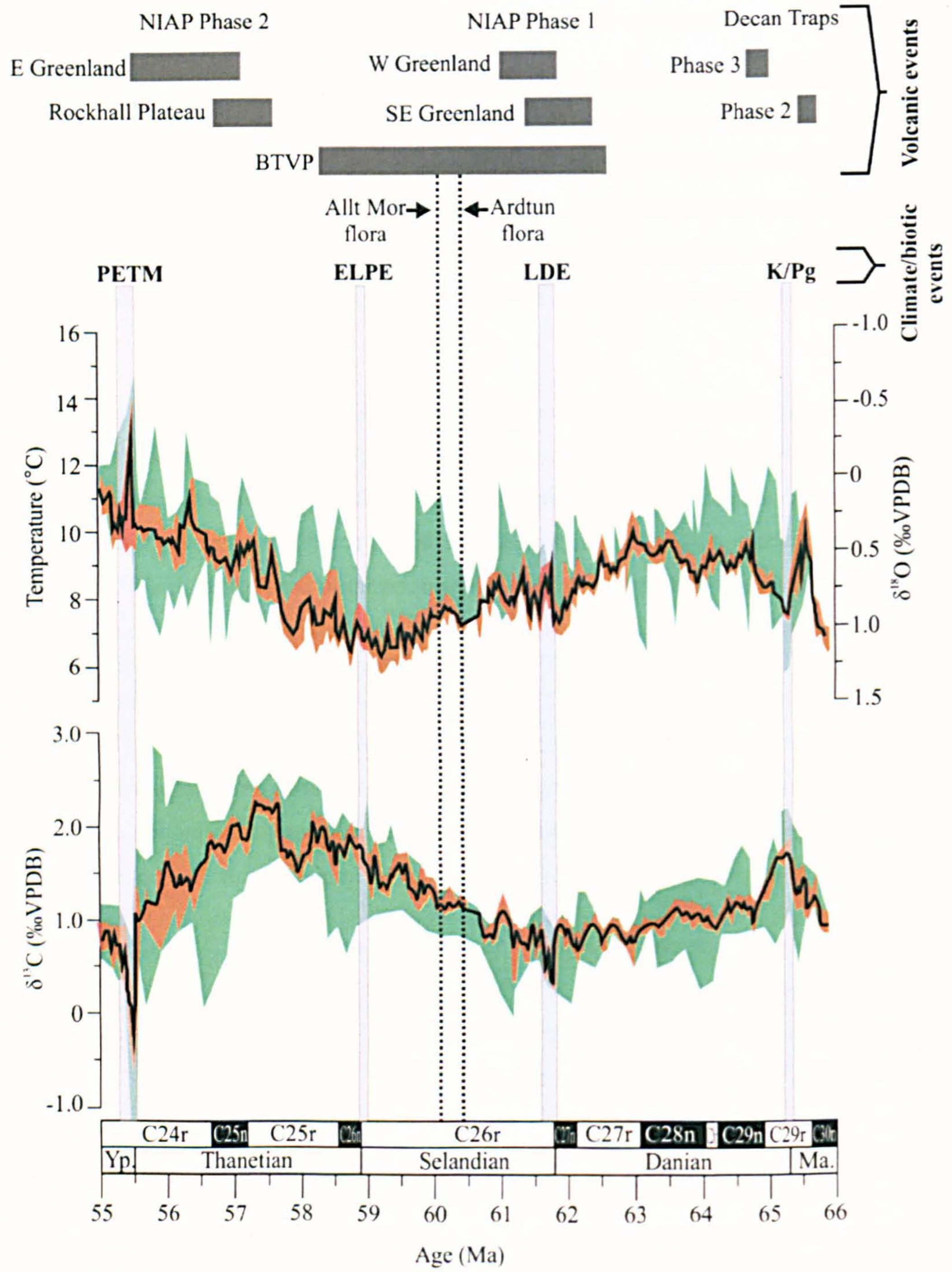

Figure 8.6. Paleocene deep-sea benthic foraminiferal δ^{18}O and δ^{13}C records from composite cores (green shaded area). Black line represents a five-point moving average of Site 1209 from Westerhold et al. (2011). The red shaded area represents values from Site 1209 only. Paleocene biotic and climatic events shown: K/Pg = Cretaceous-Paleogene boundary, LDE = Late Danian Event, ELPE = Early Late Paleocene Event, PETM = Paleocene/Eocene Thermal Maximum. The onset and duration of Deccan and NAIP volcanism (including BTVP) shown. Position of the BTVP floras of Ardtun, Mull and Allt Mor, Skye shown. Figure redrawn and modified from Westerhold et al. (2011).

The effects of the LDE hyperthermal event appear to have been short lived because ~200kyr after its onset the general cooling trend of the mid Paleocene continued (Westerhold et al. 2011). Unfortunately the oxygen isotope data for the early Selandian, the interval in which the floras of Ardtun, Mull (60.5 ± 0.3 Ma) and Allt Mor, Skye (60.16 ± 0.45 Ma) were growing is sparse compared to other intervals (Figure 8.6). Peak cooling in occurs in the late Selandian and coincides with the Early Late Paleocene Event (ELPE) and not with the BTVP floras. Benthic marine temperatures in the early at the time of the BTVP floras are, however, cooler compared to early Selandian and late Danian. This indicates that the floras of the BTVP are too old to record peak cooling in the Paleocene, but may be providing a cooling signal observed earlier in the Selandian.

8.4.3 Botanical record of Paleocene climate

The terrestrial climate record for the Paleocene has been established from physiognomic analysis of fossil floras from this interval. The floral record of North America in particular has provided an excellent climate record for the Paleocene (e.g. Wolfe 1978, Hickey 1980, Wing et al. 1995, Davies-Vollum 1997, Wing et al. 1998, Wilf 2000, Johnson et al. 2003, Wilf et al. 2003, Peppe 2010).

Mean annual temperature (MAT) estimates derived from physiognomic analysis of Northern Hemisphere floras of the mid latitudes (>30 °N to 55 °N) and low latitudes (<30 °N) sites were compiled from the literature to produce a temperature curves for the Paleocene shown in Figure 8.7. These MAT curves were then compared with the Westerhold et al. (2011) oxygen isotope curve to establish if the terrestrial and marine records provide a similar climate record (Figure 8.9).

The majority of the floral sites used in the curves are from sites from the western interior of North America, but a single site from China and the two BTVP floras were used in the mid latitude curve (Figure 8.7). The BTVP floras although a member of the Arcto-Tertiary floral zone are still mid latitude floral sites geographically, and have therefore been lumped with similar latitude floras in North America and China. The low latitude curve is composed of floras from the Mississippi Embayment area of the US (Wolfe 1978). It is important to note that MAT estimates derived from these floras were not published, but were determined here using the margin percentage scores published in Wolfe (1978). The MAT estimates were determined by applying the transfer function LMA1 to these margin percentage scores (see chapter 6 section 6.2.3 for procedure).

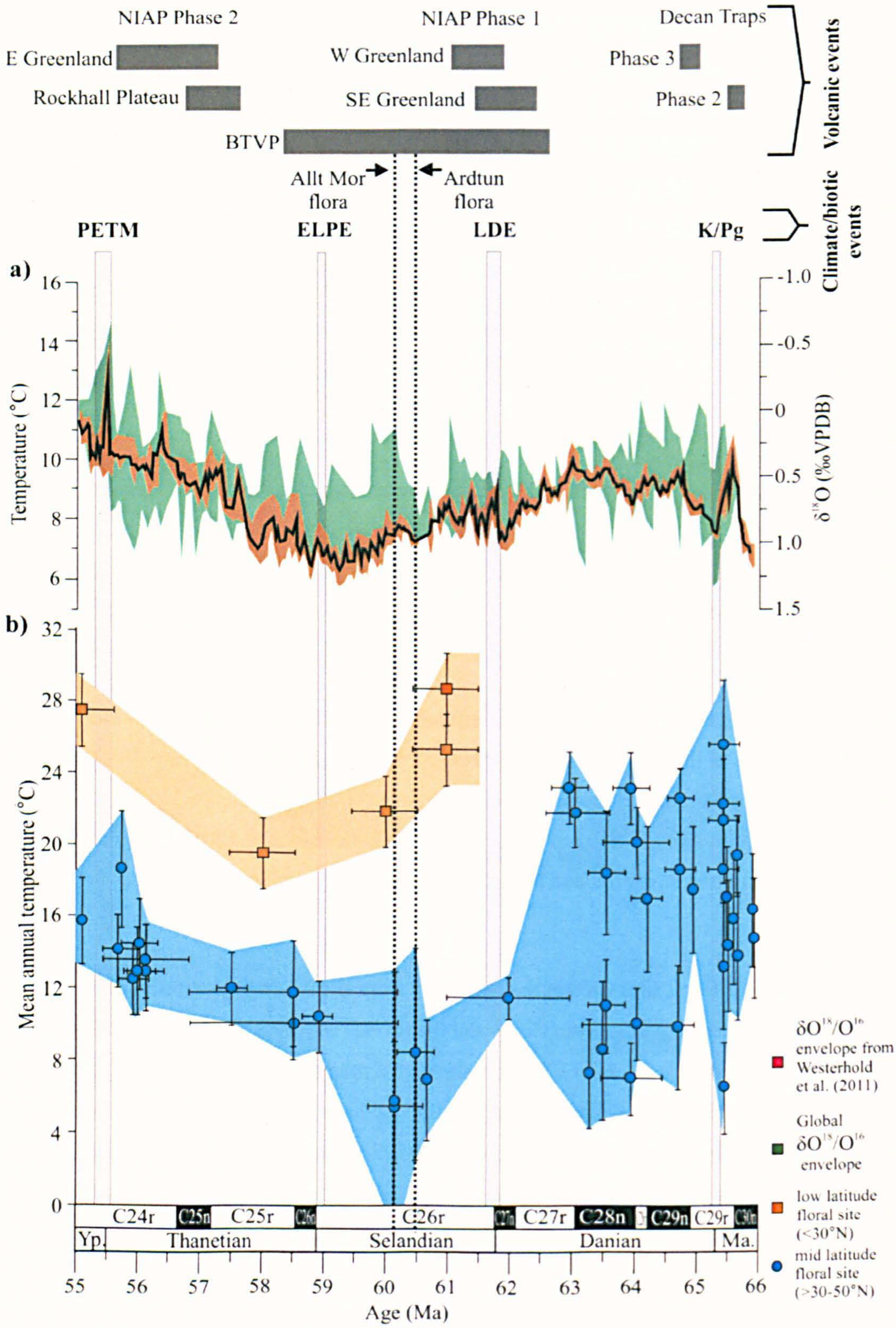

Figure 8.7. Temperature records for the Paleocene. a) Benthic marine oxygen isotope record of the Paleocene (redrawn from Westerhold et al. (2011)). Shaded red area represents data from Westerhold et al. 2011), green shaded area represents composite multisite record as in Figure 8.6. b) Mean annual temperature (MAT) estimates derived from fossil floral site in low (orange) and mid (blue) latitudes from the Northern Hemisphere. Vertical error bars represent standard error for MAT estimates, horizontal error represents dating error of floral site.

The MAT data in Figure 8.7 show that the floras of the K/Pg boundary, the earliest Danian and the latest Thanetian have been most extensively analysed, while those of the late Danian and Selandian are sparse (Figure 8.7). The general trend for the mid latitude curve indicates that the climate of the Danian was variable but generally warm, the Selandian was cooler and temperatures progressively increased in the Thanetian (Figure 8.7). The low latitude curve, although limited indicates that the climate of the Mississippi Embayment area cooled significantly through the Selandian and early Thanetian, and temperatures had reached early Selandian levels in the earliest Eocene (Figure 8.7).

The mid latitude curve shows that MAT prior to the K/Pg boundary steadily increased from ~6 °C to 12 °C to 13 °C to 19 °C at the boundary (Wilf et al. 2003). Temperatures after the boundary appear to have been cooler, which is consistent with the oxygen isotope record (Zachos et al. 2001, Westerhold et al. 2011). Figure 8.7 does not display the cooling trend after the K/Pg as clearly, as other North American floral sites appear to be significantly warmer than those obtained by Wilf et al. (2003). Estimates for the first three million years of the Danian are highly variable (Figure 8.7). This variability may be the result of climatic changes caused by the K/Pg extinction or latitudinal variation of the sample floras.

Latitudinal variation between the floras of the mid latitudes as well as regional variation in vegetation may be partially responsible for the observed variability between the temperate estimates. For example the 64.1 Ma Castle Rock flora of Colorado represents a paratropical rainforest with an MAT estimate of 22.2 ± 2 °C (Johnson and Ellis 2002), this flora is contrast with coeval vegetation in Wyoming and Montana and southern Canada, which provided MAT estimates of 6.5 ± 2.5 °C and 7.0 ± 2 °C respectively (Davies-Vollum 1997, Wolfe 1986).

The mid latitude floras have been lumped together as they occur within latitudinal range of ~30 °N to 55 °N. Due to potential changes in climate it is difficult to calculate latitudinal variation in temperatures through the Paleocene, particularly as latitudinal temperature gradients have not been adequately developed. Combing these floral estimates together may therefore provide a broader MAT signal for particular points in the Paleocene, and mask local or latitudinal variation within the mid latitudes. The absolute values may vary between sites but determining the MAT trend through the Paleocene is important to determine if the botanical record is comparable with the marine record.

The BTVP floras from Ardtun, Mull and Allt Mor Skye indicate that significant cooling occurred in the mid Selandian. The intensity of cooling between the time of the Ardtun floras and the Allt Mor flora varies depending on the physiognomic method used, differences in MAT range from 1.0 °C to 5.1 °C. Coeval floras from Williston Basin, North Dakota also indicate mid Selandian cooling, although of a lower intensity. Peppe (2010) found that MAT signal from the

Selandian Williston Basin floras decreased from 6.9 ± 3.32 °C to 5.67 ± 3.37 °C between 60.66 Ma and 60.15 Ma respectively. Younger, early Danian floras from this basin were a further 1 °C warmer, which suggests a total of 2 °C decrease from the early Danian to the mid Selandian.

The floras of the Mississippi Embayment also show this cooling trend (Figure 8.9), two floras from 61 Ma indicate tropical to subtropical conditions (28.7 °C ± 2 and 25.3 ± 2 °C) but by 60 Ma the MAT decreased to 21.9 ± 2 °C and continued to decline to 19.5 ± 2 °C at 58 Ma (Wolfe 1978). The degree of cooling between 61 Ma to 60 Ma is difficult to determine due to the standard error (sample error) but indicates MAT decreased anywhere between 10.3 °C to 1.8 °C.

The intensity of cooling obtained from mid Selandian floras appears to be highly variable regionally, the BTVP and Mississippi Embayment floras indicate that significant cooling may have occurred, while those of the Williston Basin suggest only minor cooling. This may suggest that local effects buffered or exacerbated climate cooling in the mid Paleocene.

8.4.4 Paleocene CO_2 record and climate

The concentration of atmospheric CO_2 in the Paleocene are estimated to be in the range of ~200-4000 ppmv (Ekart et al. 1999, Pearson and Palmer 2000, Cojan et al. 2000, Royer et al. 2001, Nordt et al. 2002). Stomatal index has produced some of the lowest estimates with mean estimates of ~356 ppm, indicting near-present levels of atmospheric CO_2 (Royer et al. 2001, Beerling et al. 2002, Royer 2003).

The highest CO_2 estimate was obtained from *Ginkgo gardneri* leaves from Ardtun, Mull with 826 ppm. Royer et al. (2001) suggested that the Ardtun floras were growing at 55.2 Ma during the time of the PETM, where CO_2 increased dramatically. The Royer et al. (2001) study claims the dating of this flora is uncertain, and assigned this age based on the palynological dating by Jolley (1997). The potential inaccuracies based on the palynological dating of Ardtun have been discussed in Chapter 7 (see section 7.3), which suggests the age assignment used by Royer et al. (2001) may be unreliable.

Accurate radiometric dating of the Staffa lava group, which contains the Ardtun leaf assemblage, has been dated as 60.56 ± 0.29, suggesting a mid Paleocene age (Chambers and Pringle 2001). Royer et al. (2001) tested the Ardtun sediments for the negative carbon excursion, which could assign this flora to the PETM, but were unable to detect it. The palaeoclimate estimates from this study also refute a latest Paleocene age assignment, as the temperature estimates are too low compared to temperature estimates for the PETM (Wing et al. 1998, Wing et al. 2000). The CO_2 estimates derived from the stomatal index of fossil *Ginkgo* leaves presented in Figure 8.8 have been modified from Royer et al. (2001) and Royer (2003), with the appropriate mid Paleocene age assignment as indicated by the radiometric date for Ardtun.

As to why the Ardtun *Ginkgo gardneri* leaves have provided higher CO_2 estimate relative to other estimates in the studies conducted by Royer et al. (2001) and Royer (2003) may be related to species specific variation and local volcanic sources of CO_2. The majority of CO_2 estimates presented in Royer et al. (2001) and Royer (2003) were obtained from *Ginkgo adiantoides* leaves from North America. This form of *Ginkgo* could potentially have a different response to CO_2 than *Ginkgo gardneri* of Ardrtun, Mull and may therefore, provide differing estimates of CO_2. *Ginkgo gardneri* was also growing in volcanically active environment where CO_2 may have periodically been higher than ambient levels due to volcanic degassing. It is therefore possible that the CO_2 estimates derived from the Ardtun *Ginkgo* leaves may not be comparable to those from North America. The higher estimate from Ardtun may indicate that the atmospheric levels were higher in the Paleocene than the North American record suggests.

Pedogenic carbonates have provided estimates of CO_2 levels during the Early Paleocene (Cojan et al. 2000, Nordt et al. 2002). These studies indicate that CO_2 concentrations increased rapidly towards the K/Pg boundary from ~700 ppm to 1400 ppm and declined suddenly at the boundary to ~700ppm (Nordt et al. 2002). Atmospheric CO_2 levels following the boundary show a gradual increase to ~800 ppm at ~64 Ma, and continued to increase in the Danian to ~1500 ppm at ~62 Ma (Cojan et al. 2000, Nordt et al. 2002) (Figure 8.8).

Boron istopes from planktonic foraminifera have provided CO_2 estimates for the past 60Ma (Pearson and Palmer 2000). This method indicates that there was a significant decline in atmospheric CO_2 from ~3600 ± 1000 ppm at 60 Ma to 2400 ± 1000 ppm at 58 Ma, which was followed by a gradual increase in the Late Paleocene (Pearson and Palmer 2000) (figure 8.8). This method was criticised, however, because ocean chemistry, particularly pertaining to sediment influx and ion concentrations was not fully taken into account (Demicco et al. 2003). Demicco et al. (2003) recalculated atmospheric CO_2 from Pearson and Palmer (2000) data, but incorporated marine pH into their modelling study. Estimates from this study produced CO_2 estimates that were ~1000 ppm lower than Pearson and Palmer (2000) results (Demicco et al. 2003). The trend of atmospheric CO_2 calculated by Demicco et al. (2003) was similar to Pearson and Palmer (2000), but the intensity of these fluctuations was reduced (Figure 8.8).

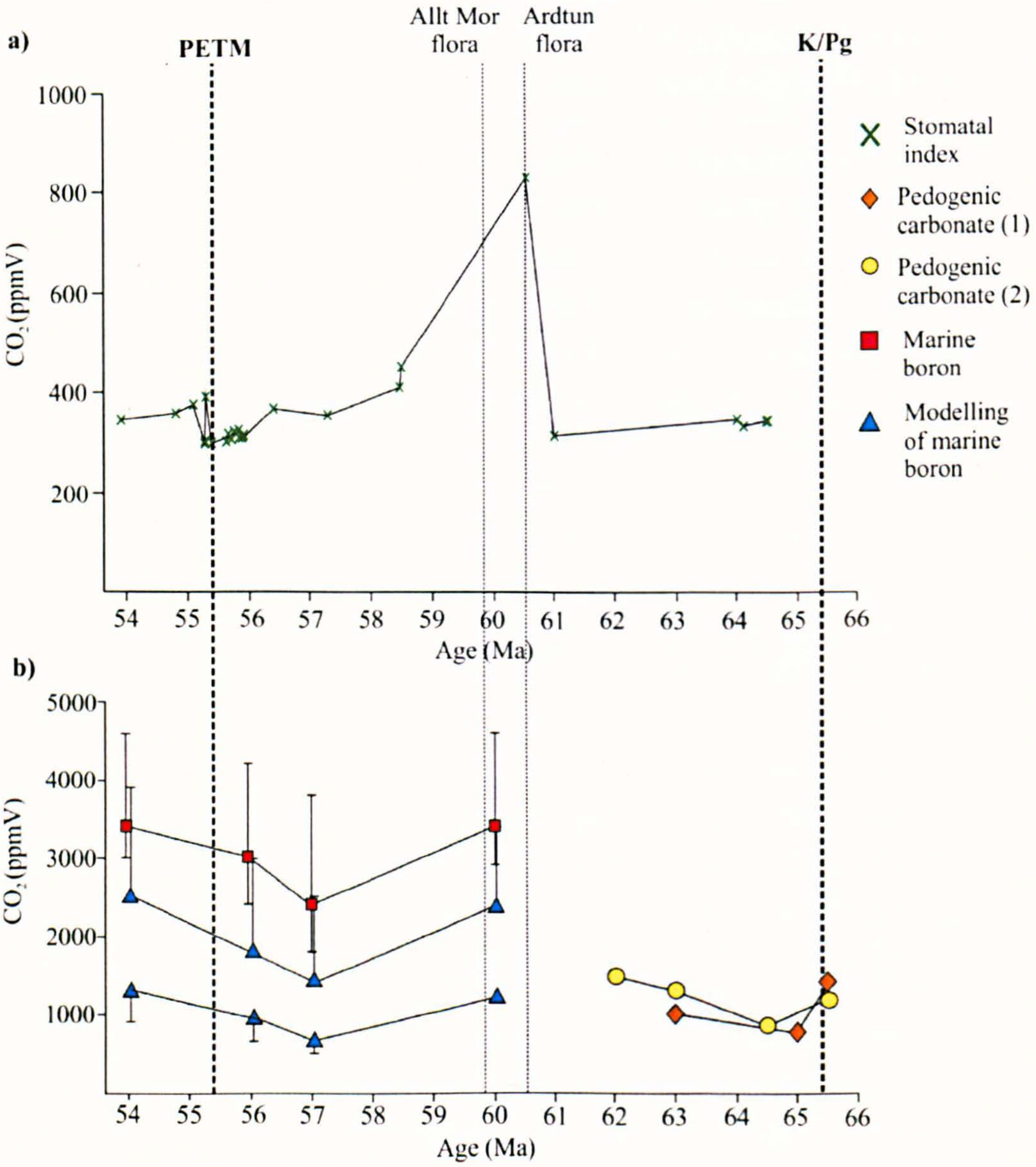

Figure 8.8. Atmospheric CO$_2$ concentrations during the Paleocene derived from multiple proxies. a) CO$_2$ estimates derived from stomatal index of fossil *Ginkgo* leaves, data from Royer et al. (2001) and Royer (2003). b) CO$_2$ estimates derived from proxies and models. Pedogenic carbonates (1) data from Nordt et al. (2002), (2) data from Cojan et al. (2000), marine boron data from Pearson and Palmer (2000), modelling of marine boron both upper and lower limits of model shown, data from Demicco et al. (2003). Position of the Cretaceous/Paleogene boundary (K/Pg), the floras of Allt Mor, Skye and Ardtun, Mull and the Paleocene/Eocene Thermal Maximum (PETM) shown.

The Paleocene atmospheric CO$_2$ record is patchy but by incorporating multiple proxies it has provided an insight into the changes in the concentrations of this greenhouse gas though this interval. Pedogenic carbonates indicate that significant changes occurred towards, during and after the K/Pg boundary. This proxy has also shown that levels of atmospheric CO$_2$ continued to increase in the Early Paleocene and reached levels that were greater than the latest Cretaceous (Cojan et al. 2000, Nordt et al. 2002). Marine boron and modelling of this CO$_2$ proxy indicate that concentrations of CO_2 declined during the mid Paleocene and early Late Paleocene (Pearson and Palmer 2000, Demicco et al. 2003). Stomatal index of fossil *Ginkgo* leaves has provided the most well sampled record of CO_2 for this interval (Royer et al. 2001, Royer 2003). The estimates derived from this proxy are, however, considerably lower than the other proxies. With the exception of the highest estimate from Ardtun, Mull the overall record of CO_2 from this proxy displays a similar trend in the fluctuations of CO_2 to the marine boron record.

The decline in CO_2 during the mid and early Late Paleocene could be linked with the observed decline in temperatures in the oceans and the botanical record from the BTVP and the Northern Hemisphere. Indeed, the decline in CO_2 could be a major factor contributing to cooling in the mid Paleocene and the cooling observed between the floras of Mull and Skye.

8.4.5 Other mid Paleocene climate proxies

Cooling in the mid Paleocene is also indicated from a variety of other climate proxies from across the Northern Hemisphere. Considerable changes in climate and weathering occurred across the Peri-Tethys at approximately 59 Ma. Clay mineral ratios show a widespread shift from kaolinite to an increase in smectite deposition (Bolle and Adatte 2000). Indicating precipitation became more seasonal, and the climate more arid (Robert and Kennet 1994). This climate shift from the warm-humid conditions of the Danian to a more seasonal and arid climate has been attributed to a cooling of the climate during the early-mid Selandian (Bolle and Adatte 2000). This qualitative climate record is valuable as it indicates that significant climate change took place in the mid Paleocene across a wide geographic region. The changes in climate in the Peri-Tethys occurred after the BTVP floras, this may suggest the climate in lower latitudes may have been slower to respond to the cooling climate.

The presence of glendonites (calcium carbonate concretions) in Paleocene marine sequences from Svalbard have been used to determine the presence of sea ice. The study by Spielhagen and Tripati (2009) indicate that sea ice formation may have occurred in the mid Paleocene in response to cooling. The presence of sea ice during the Paleocene is surprising considering the generally equable conditions of this period, but if correct it could suggest that cooling in the mid Paleocene was potentially significant at high latitudes. Dropstones in marine deposits in New Zealand during the mid Paleocene also suggest that sea ice may have existed in the Southern Hemisphere during the Paleocene (Leckie et al. 1995). The development of sea ice provides further support for intense cooling in the mid Paleocene, which is consistent with the findings from this study.

Biotic records also indicate that cooling may have had an effect on the distribution and evolution of organisms in the mid Paleocene. As discussed in Chapter 6 (see section 6.5.3) Iberian reefs and foraminifera in the Atlantic show significant changes that have been attributed to climate cooling in the mid Paleocene (Haq et al. 1977, Baceta et al. 2005, Aguirre et al. 2007). The maximum northern extent of crocodilians declined by several degrees of latitude in the mid Paleocene, which indicates climates with MAT >14 °C did not extend as far north in the mid Paleocene compared to the early and latest Paleocene (Markwick 1998, Markwick 2007). The distribution of the conifer *Metasequoia* also appears to have been affected during the mid Paleocene as its distribution declined from ~33°N to 82°N in the early Paleocene to ~42°N to 79°N in the mid Paleocene (Liu et al. 2007), which may suggest that climate cooling may have restricted the distribution of this presumably widespread species.

8.4.6 Causes and consequences of mid Paleocene cooling

The angiosperm leaves of the BTVP have provided evidence for significant cooling in the mid Paleocene. Climate cooling during this interval is also indicated in the terrestrial and marine realms (Figure 8.7), which suggests mid Paleocene cooling was global. Cooling during this period is not restricted to mid the Paleocene but extends from ~63 Ma to ~59 Ma (Figure 8.6). This suggests that a long period of climate cooling persisted in the Paleocene (Corfield 1994, Zachos et al. 2001, Zachos et al. 2008, Westerhold et al. 2011). The trigger for long term cooling is unclear, but peak cooling in the oceans occurred between ~61 Ma to 59 Ma, which coincides with a decline in light carbon in the oceans (Figure 8.6). This increase in isotopically light carbon in the mid Paleocene is linked with enhanced primary productivity in the oceans, and the terrestrial realm (Shackleton 1987, Thomson and Schmitz 1997, Oberhansli and Perch-Nielsen 1990, Corfield 1994, Kurtz et al. 2003). Enhanced primary productivity during this interval has been suggested to have led to significant carbon sequestration, which may have contributed to a decline in atmospheric CO_2 (Oberhansli and Perch-Nielsen 1990, Corfield 1994, Kurtz et al. 2003).

The cause of enhanced productivity in the mid to Late Paleocene has not been conclusively demonstrated, but North Atlantic Igneous Province (NAIP) volcanism may have been a contributing factor. In the following section the role NAIP volcanism may have had on climate cooling during the mid Paleocene is discussed. In part this may provide some insight into cooling signal obtained from the BTVP floras as well as providing mechanism for climate cooling during this interval.

Volcanism as a driver for climate cooling has been suggested in both recent history and the geological record (e.g. Devine et al. 1984, Genin et al. 1995, Zielinkski 2000, Wignall 2001). The emission of SO_2 and its conversion to sulphate aerosols, along with tephra ejected in the atmosphere can lead to atmospheric cooling (e.g. Rampino and Self 1992, Zielinkski 1996, Thordarson and Self 2003). Volcanic emissions can lead to cooling through two mechanisms, firstly through direct scattering and absorption of solar radiation and secondly through altering cloud microphysical properties, i.e. affecting the density and lifetime of clouds in the atmosphere (Haywood and Boucher 2000, Penner et al. 2001). Cooling induced by volcanism, however, is generally short lived as tephra and sulphate aerosols are deposited from the atmosphere within days to years after to the eruption. They are therefore more likely to affect short-term climate change (Wignall 2001). Prolonged, large scale, repeated eruptions produced by Continental Flood Basalts (CFBs) such as the NAIP may have the potential to drive longer-term climate cooling (Self et al. 2005, Self et al. 2006).

The impacts of volcanism on local climate have been investigated for the 1783 to 1784 AD eruption of Laki in Iceland by examining historical records and modelling the impacts of this eruption (Thordarson and Self 2003, Stevenson et al. 2003). The findings from these studies indicate that during the time of the Laki eruption, and for four years following the eruption temperatures decreased in Iceland. The winter of 1783/1784 was particularly severe, and the coldest for ~250 years with temperatures often falling below -15 °C. The 1784 summer was also cold with frequent night time temperatures falling below freezing (Thordarson and Self 2003). Thordarson and Self (2003) found that the three years following the Laki eruption were 1.3°C to 1.4 °C cooler than the 31 year mean.

Findings from these studies may indicate that volcanically induced cooling can have a profound impact on the local climate. The eruption of BTVP and NAIP lavas could have also had a similar short-term impact on the local climate. Although these climatic perturbations may have been short-lived they may have been have been of greater magnitude because of the scale of the eruptions. Progressive large scale eruptions in the BTVP may have favoured vegetation that was able to cope with periods of low temperatures particularly in the winter, when severe frosts may have occurred due to volcanism. Vegetation that was unable to cope with these periods of cold during volcanic activity may have declined or died out in the BTVP.

This could account for the disparity between the palaeoclimate estimates and floral compositions of Allt Mor, Skye and Ardtun, Mull. The Ardtun flora was growing prior to the development of the major plateau lava sequences of the Hebrides, while the Allt Mor floras was growing during the development of the Skye Lava Group and Mull Lava Group. The younger Allt Mor flora provided MAT and CMMT estimates that were significantly cooler than those of Ardtun. The floral composition of Allt Mor is also different, this flora contains a higher proportion of conifers and deciduous angiosperms, which may have been more tolerate of cooler conditions. The Ardtun flora shares several of elements of the Allt Mor flora, but also has forms such as *Amentotaxus gladifolia* and *Camptodromites major*, which may have been less tolerant of frosts.

The onset of NAIP volcanism between 62 and 61 Ma resulted in the development of extensive lava sequences in west and southeast Greenland, Scotland and Northern Ireland (BTVP)

(Eldholm and Grue 1994, Saunders et al. 1997, Storey et al. 2007). The initiation of volcanism corresponds with the decline in temperatures following the Late Danian Event (LDE) observed in the marine record (Figure 8.6). The cooling trend in the oceans and the increase heavy carbon begin to terminate after the cessation of BTVP volcanism (Figure 8.6). It is therefore possible that the first phase of NAIP volcanism may have been a contributing factor to cooling in the mid Paleocene. The hiatus in volcanism between NAIP phase 1 and phase 2 may have been the cause of warming in the Late Paleocene.

Volcanic eruptions may only have a relatively short-term impact on climate, but their effects on the biosphere may result in longer-term cooling. Continental flood basalt volcanism has been linked with mass extinctions, which may indicate their impact on the biosphere can be severe (Wignall 2001). The NAIP, however, does not correspond to any major extinction events, despite the scale of the eruptions (Wignall 2001). This suggests that NAIP volcanism may not have had such a negative effect on the biosphere. Indeed, NAIP volcanism may have had a more positive impact to biosphere, which may have increased primary productivity.

The introduction of iron into the oceans from volcanic tephra may enhance phytoplankton growth, as iron is often limiting in marine ecosystems. The effect volcanically sourced iron may have on marine productivity is still unclear, but it is potentially a major contributing factor to the enhancement of productivity in the oceans (Duggan et al. 2010). The introduction of iron into the oceans derived from NAIP ash deposition could have potentially enhanced marine productivity in the mid Paleocene. This process could have led to significant carbon sequestration and may have been a major sink for atmospheric CO_2, thus leading to climate cooling.

Gauci et al. (2008) modelled the impacts of the 1783–1784 Laki eruption had on Northern Hemisphere wetlands and found that during the first 12 months of the eruption methane fluxes declined by 50%. The reduction in methane was the result of increased water acidity caused by sulphate deposition and reduced biological activity caused by cooler temperatures (Gauci et al. 2008). If NAIP volcanism caused similar feedbacks to Paleocene wetlands it may have contributed to climate cooling, by reducing methane emissions. Wetland environments in the BTVP would have been greatly affected due to their proximity to the eruptions, and methane produced from these wetlands may have declined significantly.

High atmosphere aerosol loading caused by volcanic eruptions increases the amount of diffuse radiation that enters the atmosphere through forward scattering, which has significant effect on photosynthesis (Mercado et al. 2009). Mercado et al. (2009) modelled the effects SO_2 emissions produced by the 1991 Mt Pinatubo eruption and anthropogenic sources had on photosynthetic rates. Their study showed that photosynthetic rates increased following the eruption of Mt

Pinatubo in 1991, which enhanced terrestrial primary productivity for 2 to 3 years following the eruption. This greatly altered the global carbon sink, as increased photosynthesis effectively locked more light organic carbon from the atmosphere after the eruption. BTVP floras may have also experienced this enhanced productivity, but the proximity of the eruptions may have had more negative impact on the vegetation, thus offsetting any benefits.

During the mid Paleocene much of the mid to high latitudes were densely forested. If photosynthetic rates were enhanced by NAIP volcanism they may have created a significant carbon sink, which may have contributed to climate cooling. Indeed, the marine carbon isotope record indicates that marine primary productivity increased significantly during the onset of volcanism (Figure 8.6) and reached its highest levels for the Cenozoic (Zachos et al. 2001). Indicators of marine productivity, such as black shales are sparse in the Paleocene (Kurtz et al. 2003). This indicates that the increase in productivity, as indicated by marine carbon record, was not in the marine realm, but may have been terrestrial. The formation of coals and soils in terrestrial environments could be the primary sites of carbon sequestration during the Paleocene (Oberhansli and Perch-Nielsen 1990, Kurtz et al. 2003). Indeed, Oberhansli and Perch-Nielsen (1990) have postulated that the decline in temperatures in the mid Paleocene caused an expansion of Arcto-Tertiary floras, which were suggested to have been greater accumulators of biomass compared to the more thermophilic vegetation.

The production of CO_2 over progressive eruptions may have had the potential to counteract these cooling feedbacks. Levels of atmospheric CO_2 during the mid Paleocene, however, indicate that CO_2 declined during this interval (Figure 8.8). Indeed, CO_2 may not have increased until later in the Paleocene, perhaps after NAIP volcanism. This may indicate that primary productivity and carbon sequestration was removing more CO_2 from the atmosphere than was being emitted by NAIP volcanism.

The introduction aerosols and tephra into the atmosphere from NAIP volcanism would have had strong, but short term impact on climate cooling. The indirect feedbacks to biosphere caused by volcanism, however, may have contributed to long-term cooling in the mid Paleocene. The enhancement of primary productivity and carbon sequestration in the terrestrial realm, coupled with reduction in methane emissions from wetlands caused by periodic volcanism, and enhanced phytoplankton productivity in the oceans may have contributed to progressive cooling by sequestrating carbon and reducing atmospheric CO_2.

Subsequent eruptions and introduction of aerosols and tephra into the atmosphere may have continued to bolster these feedback mechanisms during the development of the NAIP, with the net effect being long-term cooling by reducing atmospheric CO_2 and methane. These feedback mechanisms may have contributed to the changes in floral composition and lower temperatures observed in the floras of the BTVP. This hypothesis is partly confirmed by the link between the decline in NAIP volcanism and the rise of global temperatures and atmospheric CO_2 (Figure 8.7, 8.8). This suggests that volcanism could be a key component of mid Paleocene cooling. It is possible that cooling in the mid Paleocene was caused by other mechanisms that have not been identified, but NAIP volcanism may have exacerbated the cooling trend in the Paleocene. Regardless of the causal mechanisms mid Paleocene climate cooling appears to be responsible for the differences in composition and climate observed in the floras of Ardtun, Mull and Allt Mor, Skye.

8.4.7 Summary

The climate estimates obtained from the angiosperm leaf morphotypes of the BTVP have indicated that rapid and pronounced cooling occurred in the mid Paleocene. Comparisons with marine oxygen isotope record support these results, as benthic temperatures also show a marked decline during this interval (Zachos et al. 2001, Zachos et al. 2008, Westerhold et al. 2011).

By compiling MAT estimates derived from leaf physiognomy from Northern Hemisphere floras it was possible to reconstruct the terrestrial climate record for the Paleocene. The botanical record appears to correlate with the marine record and shows many of the climatic trends observed in the marine oxygen isotope record. This suggests that Paleocene vegetation particularly that from North America has provided a reliable record of terrestrial temperatures for this interval. Mid Paleocene floral sites from mid and low latitudes in North America indicate cooling occurred, which supports the results from this study.

Atmospheric CO_2 records show a decline during the mid Paleocene and may correlate with a cooling trend. Other independent proxies and biotic records indicate that cooling during the mid Paleocene was global and had an impact on a wide variety of organisms.

The causes of mid Paleocene cooling may be linked to enhanced productivity in the mid Paleocene, which may have been the result of feedbacks from NAIP volcanism. The introduction of significant quantities of volcanic aerosols and tephra into the atmosphere may have had a strong but short term impact on the climate. However, indirect effects to the biosphere that resulted from volcanic eruptions may have led to progressive cooling through enhanced productivity, carbon sequestration and subsequent decline in greenhouse gases during the mid Paleocene. These feedbacks may have been a significant factor that changed the floral composition of western Scotland from a warm-temperate flora to a cool-temperate flora.

8.5 Chapter summary

The floras of the BTVP have provided an important insight into Paleocene vegetation and palaeoclimate of northwest Britain. The composition of these floras indicates that they are most similar to floras of the Arctic, and appear to be part of the Arcto-Tertiary floral zone. Why these floras had a more temperate, Arctic aspect and not a subtropical aspect like coeval floras in Europe may be linked to climate cooling. The decline of global temperatures during the mid Paleocene may have promoted the southward migration of vegetation from the Arctic into the BTVP. Volcanism in this region may have contributed to this cooling and further promoted the southward migration of lower temperature tolerant vegetation, while preventing thermophilic vegetation from migrating northward.

Floras that reached the BTVP via the North Atlantic land-bridge would have had to cope with the volcanic environments of the BTVP. The BTVP may have been a hostile environment to vegetation as it may have been nutrient poor, prone to disturbance and eruptions may have led to short-term, but severe declines in temperature. The floral record, however, indicates that the vegetation was not just able to cope with these factors but was able to flourish in the volcanic environments of the BTVP. Indeed, the floras may have adapted through time to cope with lower temperatures caused by volcanic eruptions, as indicated by the changes in flora composition from the Ardtun and Allt Mor floras.

A period of major floral interchange took place between Europe and North America during the late Paleocene and Early Eocene (Manchester 1999). This period of floral interchange coincides with global warming during this interval, which may have facilitated the expansion of vegetation northward. The climate cooling in the mid Paleocene may have therefore acted as a barrier to thermophilic floral elements from mixing between Europe and the rest of the Northern Hemisphere as the climate in the BTVP may have been too cool to support such vegetation during this interval. This period of cooling and volcanism in the BTVP may have prevented an earlier expansion and interchange of vegetation in the Northern hemisphere.

Chapter 9: Conclusions

New collections of mid Paleocene fossil floras from the Isle of Skye, Scotland have been investigated to determine their composition, vegetation structure and palaeoclimate. This study is the first to describe these plant fossils and determine the palaeoclimate information they provide. The fossil floras of Skye have also provided insight into their relationship with the previously-described floras of Ardtun, Mull, and floras from other localities in the British Tertiary Volcanic Province (BTVP). This comparison has provided information that has helped reconstruct the vegetation composition and structure, and its variation across the BTVP during the Paleocene. Furthermore, these floras have provided not just information on vegetation and palaeoclimate of Skye but have contributed to the understanding of the floral and climate history of the Northern Hemisphere during the Paleocene.

In response to the questions that were raised in section 1.6.1 a summary of the major findings of this study are presented below.

9.1. Summary of major findings

1. **What are the main botanical components of the fossil floras of Skye?**
   i) The fossil floral remains present in the Skye plant assemblages include a variety of broadleaved angiosperms and conifers. Fourteen angiosperm morphotypes have been identified from the Allt Mor assemblage. Eleven of these morphotypes have been identified as previously described fossil taxa and show similarities to modern members of the Platanaceae (AM1 *Platanites hebridicus*), Cercidiphyllaceae (AM2 *Trochodendroides antiqua*), Betulaceae (AM3 *Corylites hebridicus*, AM4 "*Corylites* cf."), Fagaceae (AM5 *Fagopsiphyllum groenlandica*), Juglandaceae (AM6 *Juglandiphyllites* sp.1, AM7 *Juglandiphyllites* sp2, AM8 "*Platycarya* cf."), Vitaceae (AM9 *Vitiphyllum sewardii*), Cornaceae (AM10 *Cornophyllum hebridicum*) and Trochodendraceae (AM11 *Zizyphoides* sp.). The three remaining angiosperm morphotypes of Skye (AM12, AM13 and AM14) are too poorly preserved to determine their taxonomic affinity and are considered to be enigmatic.
   ii) Conifer fossils are an abundant component of the Allt Mor assemblage of Skye, and three ovulate cone types and eight shoot morphotypes have been recognised. These cones and leafy shoots indicate that two conifer families were present on Skye during the Paleocene - the Cupressaceae and Pinaceae. Seven of the shoot morphotypes and all three ovulate cone types are attributed to the Cupressaceae, these floral remains indicating that seven genera were present, including *Metasequoia* (OC1 and CM1), *Sequoia* (OC2 and CM2), *Glyptostrobus* (CM3),

"*Chamaecyparis* cf." (CM4), "*Thuja* cf." (CM5), *Mesocyparis* sp. (CM6) and "*Calocedrus* cf." (CM7).

iii) Published palynological evidence indicates that ferns also grew on Skye during the Paleocene (Jolley 1997).

2) **What can these fossils tell us about the composition and ecosystem structure of the Paleocene BTVP vegetation?**

i) The Allt Mor plant assemblage contains abundant conifer and broadleaved angiosperm fossils, which indicates that mixed coniferous forests developed on Skye during the mid Paleocene. These mixed coniferous forests appear to have been dominated by climax conifers with an understorey of woody angiosperm trees and shrubs.

ii) A large proportion of the floral elements of the Allt Mor assemblage are considered to be rare elements of the flora (<1 %), their rarity possibly related to their limited preservation potential, or because they may have grown further away from the site of deposition or may have been truly rare elements of the flora. Rarefaction curves of the of the Allt Mor flora indicate that the collection effort in this study was sufficient to sample the diversity of the assemblage. The rarity of many of the floral elements may therefore indicate that vegetation was heterogeneous.

iii) The Allt Geodh' a' Ghamhna and Glen Osdale plant assemblages of Skye have provided only a limited number of specimens. In these assemblages only angiosperm leaves are recognisable. This suggests that these assemblages represent angiosperm-dominated riparian vegetation, similar to some components of the Allt Mor assemblage.

iv) The published palynomorph record of Skye (Jolley 1997) confirms that the macrofossil components of the Skye plant assemblages were represented in the pollen record. The study by Jolley (1997) although comprehensive in the number of sites sampled, was hindered by the poor preservation of the palynomorphs. The macrofossil record, although more biased to local vegetation appears to be representative of the regional vegetation.

v) The picture of the vegetation that has emerged from the Skye floral assemblages and palynomorph record indicates that the vegetation of this region varied spatially in response to disturbance (both flooding and volcanic), topography and drainage. The less disturbed environments appear to have developed into climax, mixed, coniferous forests, with taxodiaceous types dominating in the lowlands and pines in the more elevated areas. Areas with greater disturbance intensity or frequency such as riparian environments and the lava fields of the BTVP may have been more angiosperm-dominated.

3) **How are the floras preserved within the volcanically dominated terrain of the BTVP, and what does this tell us about the palaeoenvironments in the lava field setting?**
   i) The angiosperm and conifer fossils of Allt Mor appear to have accumulated in a pond environment that developed on the lava surface. The fragmentation of the angiosperm leaf specimens and their size indicates that they represent both parautochthonous and allochthonous elements. The parautochthonous elements represent marginal vegetation growing around the pond deposit and vegetation that was growing close by. The allochthonous component of the flora appears to have been transported by rivers and flood events, which deposited the leaf remains into the pond. The Allt Mor flora is dominated by local floral elements, but the transported component of the flora has preserved the more regional vegetation as well.
   ii) The Allt Mor flora represents vegetation that grew in palaeovalley, which was drained by a braided river system. Within this palaeovalley a variety of fluvio-lacustrine environments developed, which in turn supported different plant communities.
   iii) The vegetation growing on the valley sides and tops was probably dominated by conifers such as *Metasequoia*, *Sequoia*, members of the Cupressoideae (CM4 to CM7) and members of the Pinaceae (CM8). These conifers appear to have colonised the valley floor and the less disturbed sections of the floodplains, as their remains are common in the Allt Mor assemblage, particularly *Metasequoia* and *Sequoia*.
   iv) The more disturbed sections of the floodplains and channel margins appear to have been dominated by woody angiosperms, in particular *Platanites*, *Trochodendroides*, *Corylites* and "*Platycarya* cf.". These angiosperm taxa may also have grown within the more conifer-dominated patches of forest, as the understorey.
   v) Waterlogged swamp or marginal lacustrine environments appear to have supported both angiosperms and conifers, in particular *Metasequoia*, *Glyptostrobus* and members of the Platanaceae, Cercidiphyllaceae, Betulaceae and Juglandaceae.

4) **How does the new flora from Skye compare with the well known flora from Mull?**
   i) The well studied flora of Ardtun, Mull contains many taxa that are also present in the Skye assemblages (see Chapter 7, Table 7.9 to 7.10), but includes elements that have not been found on Skye. Herbaceous elements, such as the fern *Onoclea*

hebridicus and *Equisetum*, have been identified in the Mull assemblages. Gymnosperms, such as *Ginkgo gardneri* and *Amentotaxus gladifolia*, are relatively common at Ardtun but have not been found in the Skye assemblages in this study. The angiosperm component of the Ardtun flora has several species that are not present on Skye, including *Camptodromites major*, *C. multinervatus*, *Davidoidea hebridica*, *D. ardtunensis*, *Cupuliferites rubrifolius* and *Zizyphoides ardtunensis*.

ii) The floral assemblages of Skye and Mull were formed in fluvio-lacustrine environments, which are broadly similar between these sites. Despite developing in a similar palaeoenvironment the vegetation structure of Ardtun, Mull differs markedly to Allt Mor of Skye. The Ardtun flora represents an angiosperm-dominated community and the conifers that are important in the Skye assemblage are either rare components of the flora or are absent. This difference in vegetation structure has also been noted in the palynomorph record, which indicates that conifers were a minor component of the Ardtun flora, but were common elsewhere on Mull. This suggests that the vegetation of the BTVP may have been broadly similar regionally but may have locally varied. This local heterogeneity may have been the result of differences in fluvial and volcanic disturbance, topography and local climate.

iii) Another important difference between the floras is the presence of thermophilic elements in the Ardtun assemblage. These elements include *Amentotaxus gladifolia*, whose modern and past relatives are associated with warmer temperate and subtropical climates. Two angiosperms *Camptodromites major* and *C. multinervatus* also appear to be thermophilic as they have entire margins and thick coriaceous leaf textures; *Camptodromites major* in particular appears to represent an evergreen species typical of warmer climates.

5) What do the floras tell us about the prevailing Paleocene climate of the BTVP region and how it is linked to the palaeoclimates across the Northern Hemisphere?

i) The angiosperm leaf morphotypes of Skye were used to determine the palaeoclimate of Skye during the mid-Paleocene. Three physiognomic methods were used: Leaf Margin Analysis (LMA), Climate Leaf Analysis Multivariate Program (CLAMP) and Multiple Linear Regression Models (MLRs). In total, 14 separate analyses were used in this study.

ii) These physiognomic methods indicate that the mean annual temperature (MAT) of Skye during the Paleocene was between -0.1 °C to 12.9 °C, although 5 °C to 9 °C is considered a more reliable estimate of the MAT. The seasonality of the climate was determined using CLAMP and MLRs; estimates of the cold mean month temperature (CMM) range from -18.3 °C to 4.2 °C, and estimates of warm month mean temperature (WMM) range from 19.0 °C to 25.8 °C, however the CLAMP estimates of CMM (-3.0 °C to 4.2 °C) are considered to be more realistic. Estimates of the growing season precipitation (GSP) were determined using CLAMP and MLRs and range from 1175.6 mm to 2266.7 mm, indicating that the climate of Skye during the mid-Paleocene was cool temperate to temperate, had seasonally cold winters and warm summers, and was humid. The palaeoclimate of Skye appears comparable to modern temperate rainforests, which is supported by the botanical composition of the flora.

iii) The variation observed using the different methods indicates that caution should be used when a single method is used to determine palaeoclimate. The anomalously high temperature estimates derived from the CLAMP analysis may indicate that this method is less reliable for Paleocene or older floras. This assertion requires further scrutiny with better preserved and more diverse floras from this interval to test CLAMP's reliability using Paleocene or older floras.

iv) The angiosperm leaf fossils of Ardtun, Mull were also analysed for palaeoclimate using the same methods. Estimates for MAT ranged from 2.5 °C to 15.5 °C, although a MAT of 7 °C to 13 °C is considered to be more representative. Estimates of CMM ranged from -9.4 °C to 5.6 °C, and for WMM ranged from 20.2 °C to 29.0 °C. The CLAMP estimates of CMM (-2.7 °C to 5.6 °C), similar to those obtained from the Skye floras, are considered to be reliable. Estimates of GSP ranged from 791 mm to 2448 mm. This indicates that the ambient climate of Mull was temperate to warm temperate, seasonal with cool winters and warm to hot summers, and was humid.

v) The palaeoclimate results derived from the floras of Skye and Mull indicate that the climate changed significantly during the mid Paleocene. The MAT estimates from Mull are 1.0°C to 5.1°C warmer than those obtained from Skye, which indicates that the climate cooled during the time interval separating the Mull and Skye floras.

vi) The age of the Ardtun flora of Mull has been questioned, radiometric dating suggests that it was mid Paleocene in age (60.6 ± 0.3 Ma), while palynological dating osuggested the flora was latest Paleocene to earliest Eocene in age (55 to 54.5 Ma). The composition of the Ardtun flora does not appear to be similar to floras of the latest Paleocene, which are associated with warmer climates. The palaeoclimate estimates for this flora obtained in this study also do not support the younger age assignment, as they are too cool compared to coeval floras in North America during the latest Paleocene. The radiometric dating of Ardtun was therefore considered to be more reliable, and the Ardtun flora of Mull is considered to be mid Paleocene in age.

vii) The palaeoclimate results derived from the BTVP floras were compared with other climate proxies from the Northern Hemisphere, which also indicate that cooling occurred during the mid Paleocene. Benthic marine oxygen isotopes indicate that cooling began at ~63 Ma and reached its lowest temperatures between 60 to 59 Ma. Mean annual temperature estimates derived from fossil floras from sites in the mid-latitudes of the western interior of the USA and the lower latitudes of the Mississippi Embayment area also show marked declines in temperature during the mid Paleocene.

viii) The cause of mid Paleocene cooling is unclear, but appears to be linked with an increase in productivity and carbon sequestration in the terrestrial and marine realms, a decline in atmospheric CO_2 and North Atlantic Igneous Province volcanism (including BTVP volcanism). The fossil floras of the BTVP have therefore provided further evidence for a distinct cool period in the mid-Paleocene prior to the intense warmth of the Paleocene/Eocene Thermal Maximum (PETM).

6) How do the BTVP floras relate to other Northern Hemisphere vegetation during the Paleocene?

i) The floras of the BTVP include representatives of common Paleocene Northern Hemisphere plant taxa such as *Onoclea*, *Ginkgo*, *Metasequoia*, *Glyptostrobus*, *Trochodendroides*, *Corylites*, *Fagopsiphyllum*, *Cornophyllum*, *Zizyphoides*, *Ushia* and *Macclinotockia*. These floral elements indicate that the BTVP had a similar character to many floral sites in the mid to high latitudes of the Northern Hemisphere, and in particular sites in Greenland, Svalbard and Canada. The similarities indicate that the BTVP floras were part of the Arcto-Tertiary floral zone.

ii) Comparisons with coeval European floras indicate that they share a few floral elements but have markedly different characters. The European floras contain more thermophilic elements and appear to have grown in subtropical or paratropical climates, compared to the more temperate conditions of the BTVP.

iii) The BTVP flora, although similar to the rest of the Northern Hemisphere, contains elements that are rare or absent elsewhere in Paleocene floras. *Platanites*, a common component of the Skye and Mull floras, has only been described from one site in Canada. Members of the Juglandaceae were a relatively common component of the BTVP floras and may indicate that this group was diversifying earlier in Europe than previously indicated. The diversity of conifers at Allt Mor is of note, as they were uncommon or absent from many European floras. Why these conifers were well established in the BTVP and not elsewhere in Europe during the

Paleocene is currently unclear, but may be due to the cooler climate of the BTVP compared to warmer subtropical or paratropical climates of Europe.

iv) The similarity of the BTVP flora with other Paleocene floras from the Northern Hemisphere indicates that vegetation was free to migrate from the Arctic and adjacent regions into northern Britain via the volcanically-active corridor of the North Atlantic land bridge. The BTVP and the NAIP therefore represented an important land corridor that enabled floral interchange between Europe and the rest of the Northern Hemisphere throughout the Paleocene. The North Atlantic was of vital importance to the significant period of floral interchange that took place in the Late Paleocene and Early Eocene. This phase of floral migration coincided with global warming, hence the cooler climates of the mid Paleocene and the relatively low temperatures of the BTVP may have, therefore, acted as barrier to thermophillic elements and may have prevented a floral interchange from taking place earlier in the Paleocene.

9.2 Future work

This study has provided an insight into the floras and palaeoclimate of the BTVP, but there is still scope further development and understanding. Several areas of research that could be improved or undertaken are briefly outlined below.

- Investigating other sedimentary sequences in the BTVP for fossil plant remains may provide additional information on the floral diversity and structure of the BTVP. Jolley (1997) noted that the Allt Mor, Carbostbeg locality on Skye contains leaf and seed fossils, so this site should be investigated for additional information on vegetation composition. These floras could also provide additional information to improve the palaeoclimate estimates.
- High resolution radiometric dating of the lavas and sedimentary sequences with the Skye Lava Group could improve the dating of the Skye floras to better date climate change during the mid Paleocene.
- In Chapter 4 the conifer fossils of the Allt Mor assemblage were described and identified. These results are preliminary because Robert Mill of the Royal Botantical Gardens of Edinburgh is conducting a detailed botanical study of the conifers. Future collaboration with Robert Mill may provide a more detailed insight into the systematic relationships of these conifers and how they relate to other conifer species in the Northern Hemisphere.

- In Chapters 6 and 7 three physiognomic analyses were used to determine the palaeoclimates of Skye and Mull. These three methods include LMA, CLAMP and MLRs, these methods produced conflicting estimates of the climate, in particular mean annual temperature. The results obtained from CLAMP were often considerably warmer than those obtained from LMA and MLR. These results highlight the importance of using multiple methods to obtain palaeoclimate information from fossil floras, and caution should be taken when only a single method is used. The reliability of CLAMP analysis for Paleocene and older floras should be investigated with greater scrutiny, and preferably with more diverse floras to ensure that this factor is not responsible for the discrepancies observed in this study.

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