Cretaceous Angiosperm Leaf Floras from Antarctica

Volume One

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The candidate confirms that the work submitted is her own and that appropriate credit has been given where reference has been made to the work of others.

CONTAINS

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Acknowledgements

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Late Cretaceous angiosperm leaf floras from the Antarctic Peninsula have been studied and described for the first time. The Hidden Lake Formation (Coniacian) and Santa Marta Formation (Santonian-early Campanian) floras were preserved within shallow marine strata exposed on James Ross Island. This area was located at approximately 65°S during the Late Cretaceous. These fossils represent the remains of vegetation growing in the southern high latitudes on an emergent volcanic arc. The plants probably grew on the delta top and along the edge of streams.

The leaf fossils are preserved as isolated and fragmentary impressions and although cuticular anatomy is not present, the angiosperm leaves show the well-preserved fine detail of leaf architecture. These leaves have been drawn and described using Hickey's (1979) terminology. Attempts were made to group the leaves into morphotypes to allow reconstruction of floral composition and palaeoclimates. Several methods of grouping leaves were used, including visual grouping, single character classification, and multivariate approaches. Multivariate statistical analysis allowed many characters to be considered simultaneously and even allowed fragmentary specimens, which were harder to deal with visually, to be evaluated. Clustering analysis was performed and dendrograms were produced for the Hidden Lake Formation and Santa Marta Formation floras, which were used in conjunction with visual assessments to group leaves with distinct morphologies into morphotypes.

A total of 41 morphotypes were identified, 30 in the Hidden Lake Formation flora and 31 in the Santa Marta Formation flora, with 20 in common. Detailed descriptions of each morphotype and representative illustrations are presented. Comparisons have been drawn with fossil and living angiosperm leaves. Architectural characteristics suggest that some of the leaves may have affinities with the Cunoniaceae, Lauraceae, Sterculiaceae, Nothofagaceae, Myrtaceae and Elaeocarpaceae. If botanical affinities can be confirmed, many of these occurrences would extend the ranges of angiosperm taxa on the Antarctic Peninsula.

Palaeoclimatic interpretation of the leaf floras included comparisons with possible nearest living relatives, analysis of leaf margins, shapes and sizes, and the application of simple linear regression and multiple linear regression models. The climate is considered to have been warm and moist. Mean annual temperature estimates of 12-21°C were provided for the Hidden Lake Formation flora and 14-23°C for the Santa Marta Formation flora. Evaluation of published data suggests that these Coniacian-early Campanian leaf floras may reflect the warmest time during the Cretaceous in Antarctica.

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1   Introduction

In studies of past environments, the polar regions are most interesting because they are most sensitive to change. Equatorial temperatures have remained fairly constant over earth history, but the polar climates have ranged from intense phases of glaciation to times of warmth and the absence of major ice caps. It is widely accepted that the Mesozoic was a time of great warmth and lower equator to pole temperature gradients (Wolfe and Upchurch 1987, Francis and Frakes 1993). The Cretaceous is significant because then there were some of the warmest episodes ever known (Barron *et al.* 1994). Although it was situated in a high latitude position during the Cretaceous, Antarctica did not have an ice cap but was covered in lush forests especially in the Antarctic Peninsula region (Francis 1999).

The interpretation of fossil plants provides an independent estimate of terrestrial palaeoclimates, supplementing the marine isotopic record. Plants are the most sensitive indicators of terrestrial climate conditions because they are not mobile and so they have to be well adapted to local conditions to survive. If not, they are either killed directly, such as by desiccation, or are outcompeted by better-adapted plants. Evidence of climate change from Antarctic fossil plants is crucial for testing predictions of computer-generated climate simulations. The study of these past greenhouse climates may provide useful information for the future if we are to cope with problems of anthropogenic warming.

This study focuses on the Late Cretaceous floras of the Antarctic Peninsula, when a diverse angiosperm component had become established within the regional flora. At this time, Antarctica was still connected to South America, Australia and New Zealand. The Antarctic Peninsula held a crucial position linking west and east Gondwana during the radiation and diversification of the angiosperms (Hill and Scriven 1995). The Turonian-Coniacian-Santonian is an important transitional time in the history of the Cretaceous Antarctic vegetation, with the appearance of new angiosperm families that went on to typify Southern Hemisphere vegetation (Askin and Spicer 1992). The southern high latitudes were a locus of evolutionary innovation from the Turonian to the end of the Cretaceous (Dettmann 1989).

There are well-preserved and diverse angiosperm leaf floras in the marine sediments of the James Ross Basin, east of the Antarctic Peninsula, which provide new useful information. Two Late Cretaceous leaf floras from northwestern James Ross Island are the focus of this project and are studied and described here for the first time. The earliest flora is from the Coniacian Hidden Lake Formation and the second is from the Santonian-early Campanian Lachman Crags Member of the Santa Marta Formation.

1.1 Thesis outline

This thesis presents results of a study of the composition of these Late Cretaceous Antarctic angiosperm leaf floras and aims to answer the following questions. Were angiosperms present in the vegetation and if so, what were the common elements? What do these fossil floras tell us about the evolution, radiation and diversification of the angiosperms? What can be deduced from taxonomic composition and plant physiognomic analysis about the Antarctic palaeoclimate?

More than 200 angiosperm leaf specimens from the Hidden Lake Formation and Santa Marta Formation floras were studied for the first time during this project. Characters such as leaf form, the style of the apex and base, marginal features, and primary, secondary and tertiary venation patterns were recorded (Chapter 3). The excellent preservation of some of these specimens also allows the description of the higher-orders of venation. Studies of leaf architecture are useful because dicotyledonous leaves have been shown to possess consistent patterns of organisation at all levels from subclass to species (Hickey 1979). Multivariate statistical methods are used here to cluster the leaves into groups with common characteristics (morphotypes) (Chapter 4). The resulting morphotypes are compared with fossil and modern leaves, and their stratigraphic distribution, to aid understanding of the role of Antarctic floras in the evolution of angiosperms across Gondwana (Chapter 5). These morphotypes are then analysed in order to provide an independent estimate of terrestrial palaeoclimates (Chapter 6). Finally in Chapter 7 the results of this study are discussed in relation to previous information about Cretaceous angiosperm evolution and palaeoclimate in Antarctica.

1.2 Geological Setting

1.2.1 Introduction

Antarctic sedimentary rocks of Cretaceous age are known from the Antarctic Peninsula area and from continental shelf sequences offshore from East Antarctica (Truswell 1990, 1991, Askin 1992, Crame 1994, Francis 1999). Exposed plant-bearing strata of Late Cretaceous-early Tertiary age occur on Alexander, Adelaide, and Brabant islands on the western side of the peninsula; on various islands in the James Ross Basin to the east; and on the South Shetland Islands in the north (Figure 1.1). Fossil remains include leaf compressions and impressions, wood, pollen and spores, dispersed cuticular material, and rarely roots and reproductive organs such as flowers, cones, fruits and seeds, all of which provide information on the high-latitude forests and their ambient environments (Birkenmajer and Zastawniak 1989a,b, Askin 1992). On East Antarctica, sedimentary sequences of Cretaceous age are unknown, concealed by the ice (Truswell 1991). There is only supplementary palynological data available from offshore drill sites and from palynomorphs recycled by glacial processes and incorporated into surficial muds on the seafloor around Antarctica (Truswell 1990).
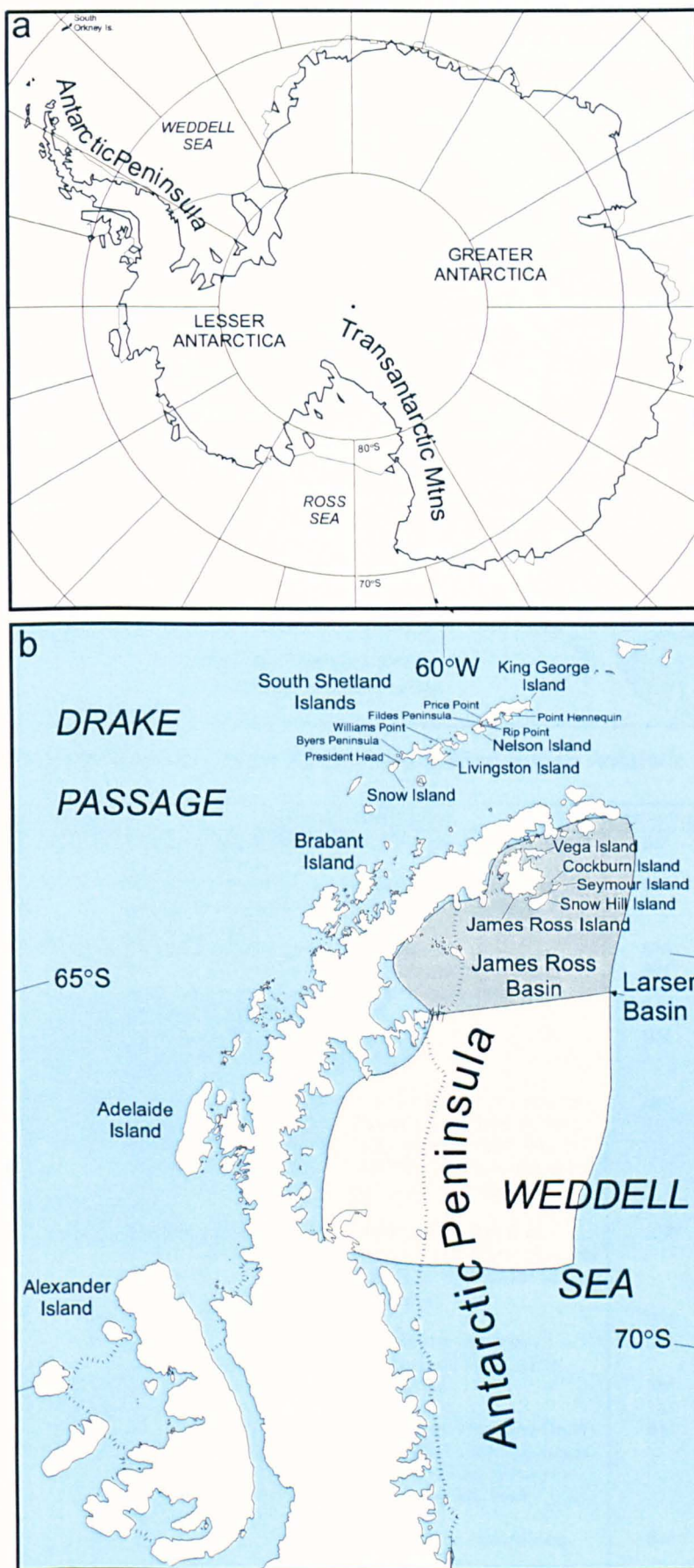
Figure 1.1 (a) Map of Antarctica. (b) Location map for the northern Antarctic Peninsula showing the limits of the Larsen Basin and the James Ross Basin. (Edited British Antarctic Survey maps with limits of sedimentary basins from del Valle et al 1992).
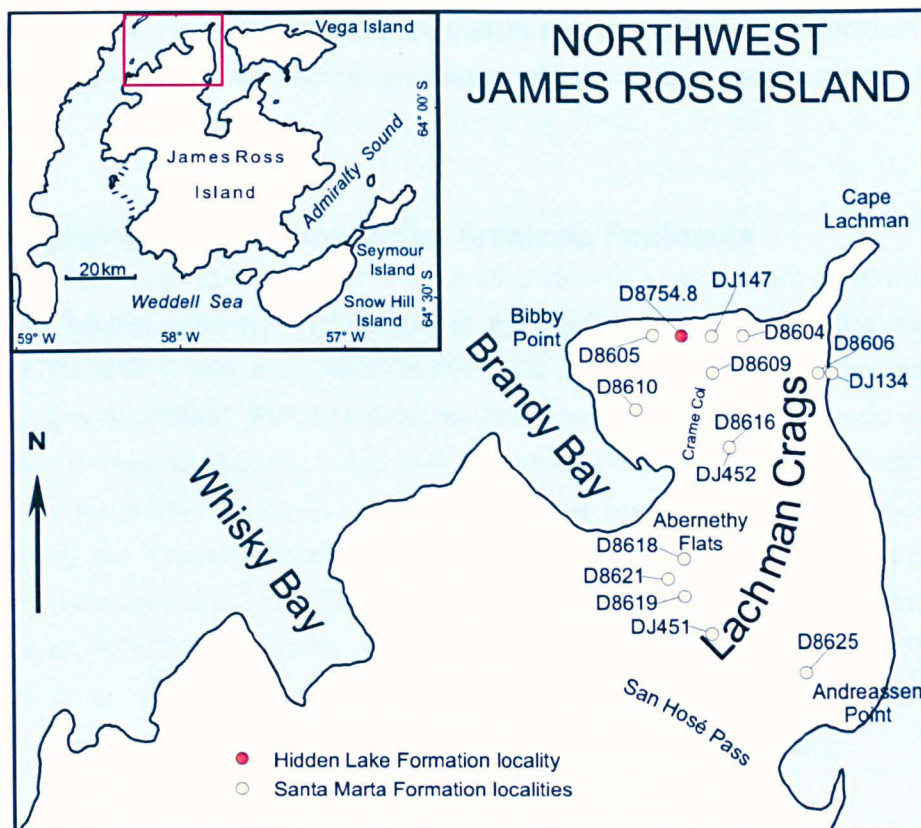
Figure 1.2 Fossil localities on James Ross Island (edited British Antarctic Survey map).

Locality	Latitude	Longitude	Locality description	Formation	Collector	Year
D8604	63.82°S	57.86°W	Bluff of sedimentary rocks on NW side of northernmost Lachman Crags.	SM	DP	1985
D8605	63.82°S	57.92°W	Small bluff on left bank of stream flowing east from Bibby Point massif. Fossils collected from single concretion bed.	SM	MRAT	1985
D8606	63.83°S	57.81°W	East side of north Lachman Crags.	SM	DP	1985
D8609	63.83°S	57.88°W	Crame Col. Stratigraphical section starting at top of snow patch on N side and working up to base of volcanic rocks on E side of col.	SM	DP	1985
D8610	63.84°S	57.93°W	Exposures of sedimentary rocks on SW side of Bibby Point massif on coast of Brandy Bay, about 3.5km SE of Bibby Point.	SM	DP	1985
D8616	63.85°S	57.87°W	Sedimentary rocks exposed below W side of Lachman Crags, about 2.5km SE of Crame Col. Stratigraphical section measured up from near valley bottom. Search for fossils, with special attention to conglomerate at top which contains rich reworked Late Cretaceous marine fauna.	SM	DP	1985
D8618	63.88°S	57.9°W	Continuation of section at D8617 about 1km S of D8617, starting at back of bowl-shaped depression and extending up to prominent triangular termination of ridge extending from SW Lachman Crags.	SM	DP	1985
D8619	63.89°S	57.9°W	SW Lachman Crags.	SM	DP	1985
D8621			Exposed in bluff below quarry (D8619); midway between that point and D8622 at 63.88°S, 57.92°W.	SM	DP	1985
D8625	63.91°S	57.82°W	SW Lachman Crags on W side of col.	SM	DP	1985
D8754.8	63.82°S	57.9°W	In a stream gully.	HL	AW	1990
DJ134	63.83°S	57.8°W	Lachman Crags between Andreassen Point and Cape Lachman. (Slope to back on E side of Lachman Crags. Same horizon probably – loose sandstone blocks in gully to beach, ~3m from beach, probably from Lachman Crags.)	SM	JEF	1989
DJ147	63.82°S	57.88°W	Crame Col, Brandy Bay. (Level of large concretions, same horizon.)	SM	JEF	1989
DJ451	63.9°S	57.88°W	San José Pass (NW side).	SM	JEF	1989
DJ452	63.85°S	57.87°W	NE side of Abernethy Flats, Brandy Bay.	SM	JEF	1989

Table 1.1 Fossil plant localities on James Ross Island.
(SM – Santa Marta Formation, HL – Hidden Lake Formation,
JEF – JE Francis, DP – Duncan Pirrie, MRAT – MRA Thomson, AW – A Whitham.)

The geological context is provided here to aid understanding of the environment in which these floras were growing, the taphonomic processes acting on the plant remains, and their preservation.

1.2.2 The geological evolution of the Antarctic Peninsula

The Antarctic Peninsula represents part of the eroded roots of a volcanic arc constructed during the east- to southeast-directed subduction of the Pacific Ocean crust along its western boundary (Elliot 1988, Crame *et al.* 1993, Crame 1994). The timing of the first emergence of this landmass is greatly debated. Based on palaeobotanical evidence, an Early Jurassic emergence of the northern Antarctic Peninsula has been proposed (Rees 1993), although controversial plant fossil evidence from the South Shetland Islands has been used to suggest the existence of land during the Triassic (Barale *et al.* 1995). Substantial thicknesses of volcanic and sedimentary rocks record Cretaceous-Tertiary volcanism, accompanied by the emplacement of plutonic bodies, migrating northwards along the length of the peninsula (Elliot 1988, Pirrie *et al.* 1991, Leat *et al.* 1995, Lawver *et al.* 1995, Dingle and Lavelle 1998). The Cretaceous angiosperm floras studied here were therefore living in an active volcanic setting.

1.2.3 The environments across the arc

This active volcanic arc was extensively forested during the Cretaceous. The Antarctic Peninsula has been divided into three tectono-stratigraphic units (Elliot 1988) representing magmatic arc, fore-arc and back-arc terrains (Figure 1.3) containing the fossil remains of these forests.
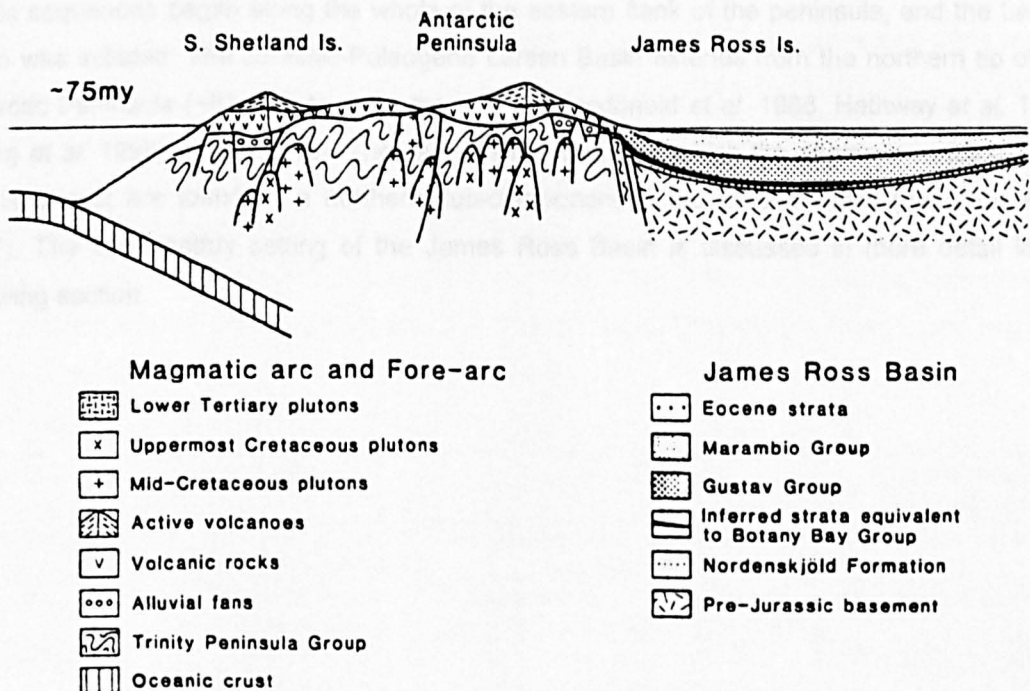
Figure 1.3. Schematic cross-section of the northern Antarctic Peninsula during the Late Cretaceous (From Elliot 1988).

There are remains of the vegetation preserved in both arc and fore-arc environments. Marginal fore-arc basin deposits are exposed on the western side of the peninsula, principally on Alexander Island, Adelaide Island, the South Shetland Islands and the South Orkney Islands (Crame *et al.* 1993, Crame 1994, Riding *et al.* 1998). Cretaceous plant remains include abundant leaves and wood within the Bajocian(?)-Albian Fossil Bluff Group of Alexander Island (Jefferson 1981, 1982a,b, 1983, Cantrill 1995, 1996, Cantrill and Nichols 1996, Riding *et al.* 1998) and common foliage and spores and pollen within Early Cretaceous Byers Group sediments on President Head, Snow Island, and Byers Peninsula, Livingston Island, (Crame *et al.* 1993, Duane 1996, Cantrill 1998).

There are Senonian to Oligocene/Miocene plant-bearing strata containing angiosperm remains in the volcanic island arc sediments, which were deposited in the South Shetland Islands (Orlando 1964, Zastawniak 1981, Stuchlik 1981, Zastawniak *et al.* 1985, Czajkowski and Rösler 1986, Francis 1986, Rees and Smellie 1989, Birkenmajer and Zastawniak 1989a,b, Li and Shen 1989, Torres and Lemoigne 1989, Zastawniak 1990, 1994, Askin 1992, Cao 1992, 1994, Chapman and Smellie 1992, Li 1994, Dutra *et al.* 1996, 1998). Birkenmajer and Zastawniak (1989a) noted that fossil leaves from this area are generally lacking in organic tissue preservation because of the heat produced by recurrent volcanic activity.

This study of Late Cretaceous angiosperms, however, focuses on the floras preserved within the back arc basin. At about 130Ma, an increased rate of subduction was reflected in extensive volcanism and major uplift and erosion of the magmatic arc with accompanying subsidence of the back-arc region (Elliot 1988, Ineson 1989, Pirrie 1991) (Figure 1.3). Deposition of coarse clastic sequences began along the whole of the eastern flank of the peninsula, and the Larsen Basin was initiated. The Jurassic-Paleogene Larsen Basin extends from the northern tip of the Antarctic Peninsula (~63.5°S) to more than 70°S (Macdonald *et al.* 1988, Hathway *et al.* 1998, Riding *et al.* 1998) (Figure 1.1b). The James Ross Basin, in which the angiosperm fossil floras in this project are found, is a northern sub-component of the Larsen Basin (del Valle *et al.* 1992). The sedimentary setting of the James Ross Basin is discussed in more detail in the following section.

1.2.4 The sedimentary fill of the James Ross Basin

The James Ross Basin provides an unparalleled record of Cretaceous marine and terrestrial life in the southern high latitudes, important in biostratigraphy, palaeoenvironments, palaeoclimates and palaeobiology (Crame *et al.* 1991, 1996, 1999, Crame 1994). This largely undeformed, predominantly shallow marine sedimentary succession, Aptian-Oligocene in age, is best exposed in the James Ross Island area (Pirrie 1991, Riding *et al.* 1998). More than 6km thick, it is the thickest exposed onshore sequence of Late Cretaceous-Tertiary sediments in Antarctica and is actually one of the thickest and most complete Upper Cretaceous-lower Tertiary sedimentary successions exposed in the Southern Hemisphere (Zinsmeister 1982, Pirrie *et al.* 1997, 1998, Hathway *et al.* 1998).

Within these sediments the remains of plants that were washed into the back arc basin from the emergent volcanic arc are relatively abundant (Francis pers. comm.). Fossil wood, (usually calcified or some coalified), is common in parts of the succession (Francis 1986, 1991, 1999, Askin 1992, Poole and Francis 1999) and there is a wide variety of leaf fossils, but much of these have not been previously documented. Abundant well preserved marine and non-marine palynomorphs provide the most continuous fossil record through this succession which, along with ammonite and bivalve faunas and isotopic studies, provides reasonably accurate dating (Dettmann and Thomson 1987, Truswell 1990, Crame *et al.* 1991, Askin 1997, Riding *et al.* 1998). The step-wise migration of terrestrial plants during the Cretaceous means that spores and pollen are less valuable in correlation and dating, so studies of microfloras of the James Ross Basin have generally focused on the dinoflagellate cysts (e.g. Keating 1992).

The Late Cretaceous-early Tertiary stratigraphy and lithology of the James Ross Island area is outlined by Ineson *et al.* (1986), Crame *et al.* (1991, 1996), Pirrie (1991), Pirrie *et al.* (1992). The siltstones, sandstones, and conglomerates of the James Ross Basin were deposited in proximal submarine fan and slope apron settings, shelf settings and deltaic environments (Dettmann and Thomson 1987, Elliot 1988). The succession is divided into three main units, the Gustav, Marambio and Seymour Island Groups. The lithology and depositional environments are summarised in Table 1.2 and Table 1.3. The geology of the James Ross Island region is illustrated in Figure 1.4a.

Group	Age	Lithology	Depositional environment
Seymour Island Group	late Paleocene-?earliest Oligocene	fine grained sandy siltstones and sandstones	shallow marine shelf
Marambio Group	Santonian-mid Paleocene	fine grained poorly consolidated sand, silt, mud and tuff sequence	shallow marine shelf
Gustav Group	early Aptian-Santonian	conglomerate-sandstone-mudstone-tuff assemblage	generally deep marine

Table 1.2 The Cretaceous-Tertiary fill of the James Ross Basin (Zinsmeister 1982, Ineson *et al.* 1986, Elliot 1988, Askin 1997, Pirrie *et al.* 1998, Riding *et al.* 1998).
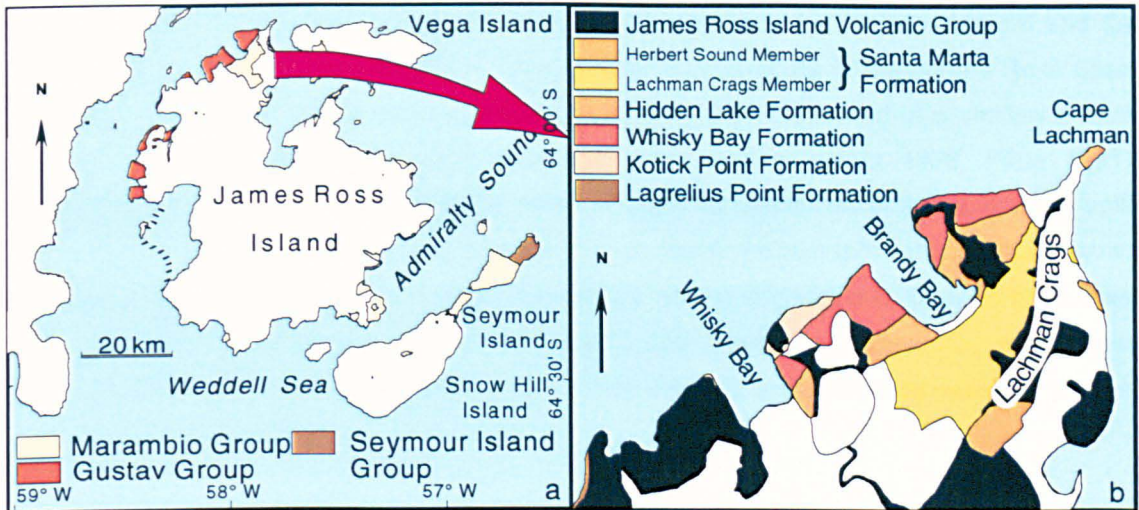
Figure 1.4 (a) Simplified geology of the James Ross Island area. (b) Simplified geology of northwestern James Ross Island. (Edited British Antarctic Survey maps, Crame and Pirrie, unpublished data. Additional geological outcrop data from Pirrie *et al.* 1992 and Crame and Luther 1997).

1.2.4.1 Gustav Group

One of the floras described in this study, the Hidden Lake Formation flora, is from the Gustav Group (see Table 1.2 and Table 1.3), so the setting is explained here. The Gustav Group represents the proximal deposition of coarse clastics by sediment gravity flows and turbidity currents along a fault controlled margin. The finer grained deposits represent environments away from the main fan channels or times of tectonic quiescence. Much penecontemporaneous volcanic material was also deposited (Ineson *et al.* 1986, Dingle and Lavelle 1998).

The Gustav Group has an age range of early Aptian-Santonian (Ineson *et al.* 1986, Riding *et al.* 1998). The outcrop areas are illustrated in Figure 1.4. Four formations are recognised within the group, the Lagrelius Point, Kotick Point, Whisky Bay and Hidden Lake Formations (Ineson *et al.* 1986). See Table 1.3 for formation descriptions, age and depositional environment.

1.2.4.1.1 Hidden Lake Formation (see Table 1.3).

Fossils from these strata form one of the two floras studied in this project. The location of these strata is illustrated in Figure 1.4b and the Hidden Lake Formation flora fossil locality (D8754.8) is shown in Figure 1.2. Within the Hidden Lake Formation there is a fining upward trend, with coarse grained volcaniclastic sandstones and channelled conglomerates with localised cross-bedding grading into burrowed sandy siltstones (Ineson *et al.* 1986). Ammonites and bivalve faunas suggested a probable age range of Coniacian-Santonian (Ineson *et al.* 1986). Samples from the beds containing the angiosperm leaf fragments studied were sent to BGS for analysis of the dinoflagellate floras. This, along with Sr isotope studies, has provided a Coniacian age for the Hidden Lake Formation (A. Crame and D. Cantrill pers. comm.).

The older beds of the Gustav Group were deposited in a deep marine environment and the Hidden Lake Formation represents the oldest shallow marine strata in the James Ross Basin (Hathway *et al.* 1998). These sand-dominated sediments were deposited in a shallow marine deltaic environment, within fan delta shelf and slope settings (Elliot 1988, Pirrie 1991). Deposition was closely related to a major pulse of proximal volcanism and probable arc uplift (Pirrie 1991, Dingle and Lavelle 1998, Hathway *et al.* 1998). Petrographic studies have shown that the distance between the sediment source and site of deposition is likely to have been small, with rapid sedimentation rates (Pirrie 1991). The plant fossils preserved within these strata, therefore, most probably originated on the volcanic arc and were washed a short distance into the marine basin.

1.2.4.2 Marambio Group

The Gustav Group is overlain conformably by the finer-grained sandstones and mudstones of the Marambio Group, deposited in a shallow marine environment (Ineson *et al.* 1986, Pirrie 1987). It includes, from the base upward, the Santa Marta Formation, the Snow Hill Island Formation, the López de Bertodano Formation, and the Sobral Formation (Crame *et al.* 1991, Riding *et al.* 1998). The area of outcrop is illustrated in Figure 1.4a.

1.2.4.2.1 Santa Marta Formation (see Table 1.3)

The Santonian-Campanian Santa Marta Formation, conformably overlying the Hidden Lake Formation, is exposed on north-western James Ross Island (Figure 1.4b). It is made up of silty and muddy sandstones with intercalated conglomerates and pelitic beds, calcite-cemented sandstones and marls, and concretionary beds (Elliot 1988, Crame *et al.* 1991). Deposition occurred within shallow marine shelf environments and petrographic and mineralogical studies indicate provenance from erosion of volcanic and plutonic elements of the Antarctic Peninsula (Browne and Pirrie 1995, Dingle and Lavelle 1998). It is divided into four members, the Lachman Crags and Herbert Sound members in the north and the Rabot and Hamilton Point Members in the south (Pirrie *et al.* 1997).

The second flora studied is from localities within the Lachman Crags Member of the Santa Marta Formation (Figure 1.4b). This member consists mainly of turbidite sandstones and intensely bioturbated silty sandstone and mudstone, with minor mass-flow conglomerates, pebbly sandstones and tuffs, and is considered to represent a mid- to outer-shelf setting, probably below storm wave-base (Pirrie 1989, Crame *et al.* 1991, Hathway *et al.* 1998). The Lachman Crags Member has been dated using molluscan faunas and dinoflagellate cysts, which have provided an early Santonian-early Campanian age (Dettmann and Thomson 1987, Doyle 1990, Crame *et al.* 1991, Keating 1992).

Many of the fossil angiosperm leaves studied are preserved within calcareous concretions, which are abundant at Crame Col, where over 300 concretions are exposed on a single bedding

plane (Pirrie 1987). The concretions commonly contain well preserved fossils including large wood fragments, leaves (JE Francis pers. comm., this study), ammonites, bivalves, crabs and gastropods, and calcareous foraminifera (Pirrie 1987). There are also calcified logs several metres long (Francis 1999, figure 4).

Following deposition of the Santa Marta Formation sedimentation continued in shallow marine conditions but leaf floras are rare in the overlying Cretaceous sediments (Francis pers. comm.).

Group	Formation	Thickness	Lithology	Age	Depositional Environment
Seymour Island	La Meseta	720m max.	uncemented silts and sands with sparse carbonate-cemented sandstones	late early/middle Eocene-?earliest Oligocene	shallow marine to intertidal delta
	Cross Valley	105m	volcaniclastic sands and conglomerates	late Paleocene	non-marine submarine canyon contemporary volcanism
Marambio	Sobral	~255m	coarsening upward silts, sands and sandstones	mid-Paleocene	delta front to top shallow shelf
	López de Bertodano	1190m	very fine sands and sandy siltstones with sparse carbonate-cemented sandstones	Maastrichtian-early Paleocene	inner and outer shelf contemporary volcanism
	Snow Hill Island	?1000m max.	mudstone dominated, ?sands with interbedded sandy clays and clays with abundant calcareous concretions	late Campanian-early Maastrichtian	inner and outer shelf
	Santa Marta	~1000m	silty and muddy sandstones with intercalated conglomerates and pelitic beds, calcite-cemented sandstones and marls, and concretionary beds containing invertebrates	Santonian-Campanian	inner and outer shelf mid-outer shelf
Gustav	Hidden Lake	>400m	coarse grained volcaniclastic sandstones and channelled conglomerates grading into burrowed sandy siltstones	Coniacian-Santonian	tidal shelf/fan-delta contemporary volcanism
	Whisky Bay	950m max.	pebble and boulder conglomerates, breccias, pebbly sandstones, sandstones and mudstones	middle Albian-Turonian/Coniacian	deep-marine fan/slope apron complex
	Kotick Point	1000m max.	monotonous thinly interbedded medium- to very fine-grained sandstones and silty mudstones or clays	Aptian-early Albian	
	Lagrelius Point	250m min.	pebble-boulder conglomerates with minor intercalations of pebbly sandstone and medium- to coarse-grained sandstone	early Aptian	deep-marine sediment gravity flow deposits

Table 1.3 Stratigraphy of the James Ross Basin (compiled from Ineson et al. 1986, Dettmann and Thomson 1987, Elliot 1988, Crame et al. 1991, 1999, Askin 1997, Pirrie et al. 1997, 1998, Dingle and Lavelle 1998, Hathway et al. 1998, Riding et al. 1998).

1.2.5 Palaeogeographic Setting

The nature and position of neighbouring land areas is important in the evolution of the Antarctic flora, determining migration routes and influencing ocean currents and climate (Wilford and Brown 1994).

Prior to 180Ma, Antarctica was joined to South America, Africa, India and Australia, making up Gondwana. Antarctica was the central piece. Since then, the continents have drifted apart, but Antarctica has maintained a high latitude polar or near polar position throughout the Mesozoic and Tertiary (Birkenmajer and Zastawniak 1989a). The pieces fit together well, except for the Antarctic Peninsula, which overlaps with South America. It is now thought Lesser Antarctica consists of several small continental blocks that moved independently of each other and Greater Antarctica (Wilford and Brown 1994). Table 1.4 shows the major events in the break-up of Gondwana.

Time	Events in the geographic evolution of Antarctica
150Ma	Movement between west (Africa and South America) and east Gondwana (Antarctica, Madagascar, Greater India and Australia) had been initiated.
140-130Ma	Initial break-up of Gondwana. Greater India, Australia and Antarctica were separating but there were no significant seaways. A landmass flanking east Antarctica and SE Australia incorporating New Zealand reached its maximum extent. Break-up between Australia and Antarctica began about 132Ma and the South Atlantic started to open at roughly this time, propagating northwards.
130Ma	Antarctica began to move past Tasmania.
120Ma	Substantial seaways between Greater India and Antarctica-W Australia and east of Africa.
110Ma	Rifting commenced between Australia and New Zealand. Rifting and rotation of crustal blocks locally affected the Antarctic Peninsula and adjacent W Antarctica until about 100Ma, but had no major effect on geography. High sea-level during Aptian and Albian allowed South Atlantic to link to the global ocean. Spreading between Australia and Antarctica allowed the proto-Indian Ocean to enter from the west, initiating the formation of the Southern Ocean.
100Ma	Erosion and subsidence reduced the landmasses around New Zealand, allowing the sea to flood a number of rift zones, but the land connection to Antarctica persisted in the south.
90Ma	About 95Ma Greater India's movement northwards rapidly increased. Slow sea-floor spreading allowed proto-Southern Ocean to extend between Antarctica and Australia 90Ma. Sea-floor spreading resulted in open ocean isolating New Zealand and New Caledonia. Subaerial volcanism existed in open ocean west of Australia between 90 and 60Ma and might have provided a 'stepping stone' for floral migration.
80Ma	Tasmania was still close to Antarctica and connected to Australia.
60Ma	Sea-floor spreading ceased in the Tasman Sea, but Australia's drift north away from Antarctica continued.
44Ma	Spreading rate between Australia and Antarctica increased forming a deep marine strait between Tasmania and Antarctica by about 38Ma. Microcontinental blocks formed a link between the Antarctic Peninsula and South America.
~30Ma	Opening of the Scotia Sea and Drake Passage finally separating South America from Antarctica allowing circum-Antarctic current to develop, but wide shelves and island chains linked both continents until Early Miocene

Table 1.4 Gondwana break up and the isolation of Antarctica.

(Information from Birkenmajer and Zastawniak 1989a, Francis and Frakes 1993, Wilford and Brown 1994).

Palaeogeographic reconstructions of southern Gondwana at 90Ma by Lawver *et al.* (1992) place James Ross Island at approximately 65°S (Figure 1.5).
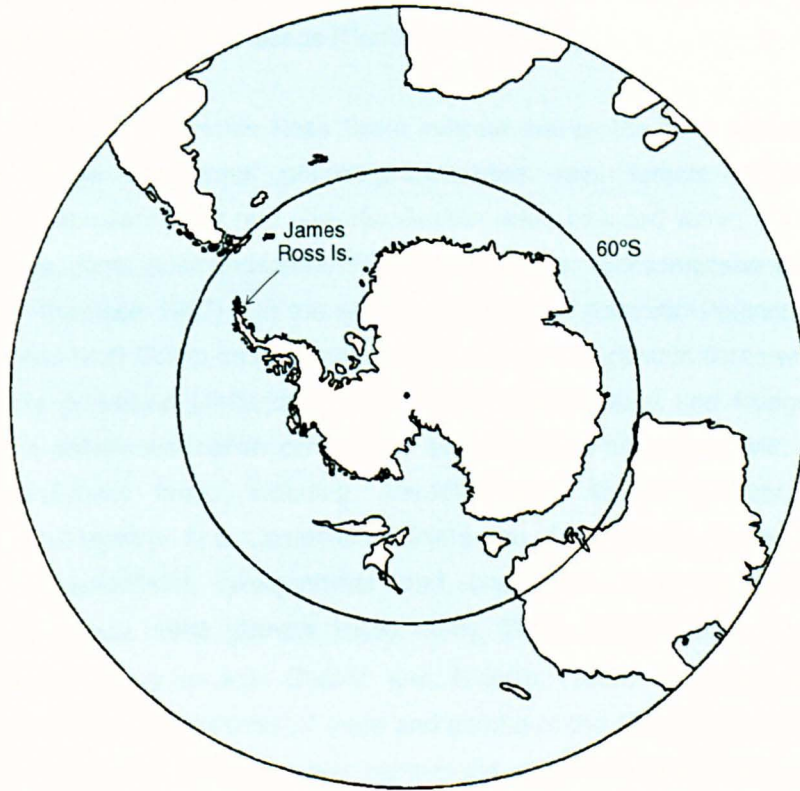
Figure 1.5 Palaeogeographic reconstruction of southern Gondwana at 90 Ma. (Redrawn from Lawver *et al.* 1992).

1.3 Cretaceous floras of the Antarctic Peninsula

There is still much work to be done on the description and interpretation of Cretaceous Antarctic floras, especially the leaf floras. Most of the information on floral composition comes from palynological data. Dettmann and Thomson (1987), Dettmann (1989), Truswell (1990, 1991), Askin (1992), Hill and Scriven (1995), Francis (1999) and others have presented reviews of the Cretaceous-Tertiary vegetation of Antarctica. Comparisons of northern and southern high-latitude floras have also been made by Askin and Spicer (1992).

The globally ubiquitous flora of conifers, ferns and cycads (Francis and Frakes 1993, Francis 1999) dominated the Early Cretaceous Antarctic Peninsula. Berriasian-Valanginian spores and pollen and fossil wood from Byers Peninsula, Livingston Island, and President Head, Snow Island (Figure 1.1), represent podocarpaceous and araucarian coniferous forests with a few cheirolepidiaceous conifers and an understorey of diverse ferns and tree ferns (Cyatheaceae/ Dicksoniaceae, Schizaeaceae, Gleicheniaceae, Osmundaceae, Lophosoriaceae), lycopods and bryophytes (Francis 1986, Truswell 1990, Duane 1996). There are fronds from a diversity of ferns, cycadeoids (*Williamsoniella*, *Ptilophyllum*, *Otozamites*, *Dictyozamites*), conifers (*Elatocladus*) and other seed plants (*Pachypteris* and *Stenopteris*) (Truswell 1990). Aptian strata on President Head also contain leaf material dominated by bennettitalean fronds, with

Pentoxylales (*Taeniopteris*), *Pachypteris*, conifers, liverworts, mosses and ferns including foliage and spores of the Lophosoriaceae (Cantrill 1997, 1998).

Palynological studies of the James Ross Basin indicate that by the early Albian, angiosperms had invaded these temperate podocarp-araucarian rain forests. Possible shrubby Chloranthaceae, represented by rare *Clavatipollenites*, were included within the understorey of diverse rain forest ferns (Osmundaceae, Hymenophyllaceae, Dicksoniaceae and *Lophosoria*) (Dettmann and Thomson 1987). On the western side of the Antarctic Peninsula, later Albian strata of the Fossil Bluff Group on Alexander Island (Figure 1.1) contain floras with tree stumps and forest floors preserved (Jefferson 1983). These diverse wood and foliage remains are interpreted as a patchy araucarian conifer and pentoxylalean overstorey with rare podocarp shrubs and dominant ferns, including *Alamatus* and *Aculea* thickets, *Hausmannia*, *Cladophlebis*, *Phlebopteris* and *Coniopteris*. There are *Elatocladus* shoots and fronds of cycadophytes (*Taeniopteris*), ginkgophytes and bryophytes such as thalloid liverworts (Jefferson 1981, 1982a, 1983, Cantrill 1995, 1996). These beds contain the oldest known angiosperm leaves in Antarctica. Cantrill and Nichols (1996) described seven species representing a scattered understorey of trees and shrubs of the Magnoliidae (Magnoliales and Laurales) and Rosidae, a small shrubby Hamamelid or Dilleniid plant and herbs showing possible affinities to the Chloranthaceae, Saururaceae, Aristolochiaceae or Piperaceae.

Through the later part of the Albian and into the Cenomanian the fossil wood and palynological assemblages of the James Ross Basin are basically similar to the earlier Albian floras. Podocarps, ferns and bryophytes are dominant, with less frequent conifers with *Brachyphyllum* foliage, Cheirolepidiaceae, Araucariaceae, Ephedrales, cycadophytes, ginkgophytes and other seed plants, but the angiosperms were increasing in diversity and frequency (Francis 1986, Dettmann and Thomson 1987, Baldoni and Medina 1989). Dettmann and Thomson (1987) reported eight pollen taxa of monocotyledonous and dicotyledonous angiosperms, some representing "higher" or non-magnoliid angiosperms, and by the end of the Cenomanian angiosperms represented 16% of the palynoflora (Baldoni and Medina 1989, Askin 1992).

Palynomorphs have indicated a Cenomanian to early Campanian age for the Williams Point Beds on Livingston Island (Figure 1.1) containing wood and leaf impressions (Rees and Smellie 1989, Torres and Lemoigne 1989, Chapman and Smellie 1992). The palynoflora is suggestive of a conifer forest with a small but diverse angiospermous element, including *Clavatipollenites*, and a rich fern and tree fern flora. The wood represents a diverse mix of conifers and scattered dicotyledonous angiosperm trees with bennettitaleans in the understorey. Some of the angiosperms would have been large trees and there are total of five wood taxa which have been compared to Magnoliales, Hamamelidae, Rosidae and in particular the Cunoniaceae (Chapman and Smellie 1992, Poole *et al.*, in press a). Rees and Smellie (1989) described six primitive angiosperm leaf types designated A to F, the most abundant of which was considered to closely resemble *Cinnamomoides*. Bennettitalean leaves (*Pterophyllum*) were also recorded. However, despite the presence of angiosperm-like leaves, Barale *et al.* (1995) still assert that

one of the Williams Point localities is in fact Triassic, based on the foliage of abundant ferns and conifers with Equisetales, Caytoniales, and Ginkgoales, which was in agreement with earlier work (Orlando 1968, Lacey and Lucas 1981).

During the Late Cretaceous many new angiosperm families started to appear, the southern podocarpaceous conifers were diversifying, and Antarctica was a locus of evolutionary novelty for many plant groups (Dettmann 1989, Askin 1992). Published data on floras from the Turonian to early Santonian are scarce (Askin 1992) and it has been suggested that the abundance and diversity of the angiosperms remained low in the Turonian-Coniacian (Dettmann 1989). Baldoni and Medina (1989) reported a palynoflora from the Coniacian-Santonian Hidden Lake Formation, James Ross Island, dominated by podocarps, ferns and bryophytes with angiosperms making up 10-16% of the flora. There are also lesser proportions of pollen of cycadophytes, ginkgophytes or other seed plants, Cheirolepidiaceae, conifers with Brachyphyllum foliage, Araucariaceae and Ephedrales. The palynofloral composition of the Santonian-Campanian Santa Marta Formation, James Ross Island, is similar, with a strong component of gleicheniaceous ferns and podocarps, but the angiosperms increase in abundance (21%) and diversity. These rocks include representatives of the Chloranthaceae, Liliaceae, Loranthaceae, Proteaceae, Casuarinaceae, Myrtaceae, Trimeniaceae, and Nothofagaceae (Dettmann and Thomson 1987, Baldoni and Medina 1989, Baldoni 1992, Keating 1992). Within the Hidden Lake Formation flora studied there is an angiospermous twig which is considered most similar to modern Cunoniaceae (Poole et al., in press a). Cunoniaceous and atherospermataceous woods have also recently been reported from the Santa Marta Formation (Poole and Francis 1999, Poole et al., in press a).

Angiospermous fossils become more abundant in the late Santonian, Campanian and Maastrichtian of the James Ross Basin and South Shetland Islands (Askin and Spicer 1992). There are leaf floras of Santonian-Maastrichtian age (Zamek Formation), on King George Island (Figure 1.1) dominated by angiosperms, with some ferns and araucarian or podocarpaceous conifer shoots. These fossils represent a rain forest community of Magnoliidae, Dilleniiidae, Nothofagus, Myrtaceae, possible Cunoniaceae and laurophyllous leaves (Birkenmajer and Zastawniak 1989a,b, Dutra 1989, 1997b, Zastawniak 1990, 1994). Campanian-Maastrichtian palynological assemblages have also been reported from Half Three Point, King George Island, with dominant ferns, rare podocarpaceous and araucarian conifers and angiosperms including Nothofagus and Loranthaceae (Cao 1992, 1994, Dutra et al. 1996). Zhou and Li (1994) have also described leaves from these strata, including fragments of Nothofagus, ferns and podocarps. Palynofloras of probable Campanian age at Price Point on King George Island contain high proportions of angiosperms, including Nothofagus and laurophyllous forms, with Ginkgoaceae and ferns (Dutra et al. 1996). At Rip Point, northeast Nelson Island, South Shetland Islands, there are leaves of possible Campanian age including abundant ferns, few conifers, Nothofagus, a Rosid or Dilleniid leaf and Magnoliid angiosperms with cinamomophyllic and laurophyllic architecture (Dutra et al. 1998).

The Campanian-Maastrichtian floras of the James Ross Basin are known from wood, dispersed cuticle and pollen records. Collections of fossil wood dominated by podocarps from the Campanian of James Ross Island contain ten angiospermous fossil wood taxa including *Nothofagus* (Francis 1991). Podocarps and *Nothofagus* are also the most abundant within palynological assemblages from the Campanian of James Ross Island and Vega Island (Figure 1.1), with ferns and infrequent Proteaceae, Myrtaceae and other angiosperms (Askin 1983, Dettmann and Thomson 1987). Angiospermous pollen is abundant and diverse by the Maastrichtian on Vega Island and approximately twelve forms of *Nothofagus*, along with other angiosperms (e.g. Casuarinaceae), were represented within podocarp-*Nothofagus* rain forest communities (Dettmann and Thomson 1987).

Palynofloras and cuticle remains on Seymour Island (Figure 1.1) record terrestrial vegetation across the Cretaceous-Tertiary boundary. Campanian-Paleocene rain forest floras are dominated by abundant podocarpaceous conifers and diverse angiosperms with a minor fern component. Angiosperm diversity increased through the latest Cretaceous, from 33 taxa in the latest Campanian to 59 in the latest Maastrichtian, with almost half the angiosperm species endemic to the Antarctic region by the end of the Cretaceous. *Nothofagus* was not yet dominant within the vegetation and other angiosperms included Proteaceae, Myrtaceae, Lauraceae, Loranthaceae, Bombacaceae, Olacaceae, Sapindaceae, Casuarinaceae, Aquifoliaceae, Gunneraceae and Ericales with rare Chloranthaceae and Liliaceae. Certain angiosperms did disappear towards the end of the Cretaceous but there is no evidence of an abrupt extinction event in the terrestrial vegetation. Instead there is a long term floral turnover with decreasing diversity in the Paleocene consistent with climate cooling (Askin 1988a,b, 1989a,b, 1994, Upchurch and Askin 1990, Crame 1994, Askin and Jacobson 1996).

Angiospermous vegetation, dominated by *Nothofagus* and laurophyllous plants, continued into the Tertiary on King George Island (Birkenmajer and Zastawniak 1986, 1989a,b). Through the Tertiary floral diversity generally declined but an amelioration of the climate in the early-middle Eocene allowed warmth-adapted plants to recolonise the northern peninsula. Floras from this period on Fildes Peninsula, King George Island, comprise podocarp-araucarian-*Nothofagus* forests, with a diversity of ferns and angiosperms (e.g. Proteaceae, Myrtaceae, Melastomataceae, Araliaceae, Anacardiaceae) (Orlando 1964, Czajkowski and Rösler 1986, Troncoso 1986, Li and Song 1988, Birkenmajer and Zastawniak 1989a,b, Li and Shen 1989, Cao 1992, Li 1994). Dusén (1908) had already identified many of these elements in leaf floras from the Eocene of Seymour Island. Other late Eocene-early Oligocene leaves, wood and pollen floras have been recorded from King George Island and Seymour Island (e.g. Stuchlik 1981, Case 1988, Torres *et al.* 1994, Askin 1997), but there was a progressive reduction in plant taxa through the Oligocene. One of the last surviving floras on the Antarctic Peninsula is of Oligocene-Miocene age from Point Hennequin, King George Island, including podocarps and *Nothofagus*, but none of the laurophyllous or sterculiaceous leaf forms characteristic of earlier warmer times (Zastawniak 1981, Zastawniak *et al.* 1985, Birkenmajer and Zastawniak 1989a,b). The falling temperatures and increased isolation inhibited the return of extensive vegetation to

Antarctica but, although the Pliocene age of the twigs and leaves is disputed, there are reports of *Nothofagus* surviving as a small alpine shrub in the Transantarctic Mountains (Figure 1.1) (Francis 1990, 1999, Hill *et al.* 1996).

1.3.1 Summary

The Early Cretaceous (Berriasian-Aptian) Antarctic flora of bryophytes, lycopods, ferns, cycads, conifers and other gymnosperms is known from the South Shetland Islands. The first evidence of angiosperms entering the podocarp, araucarian and fern rain forests of the Antarctic Peninsula is from early Albian pollen samples from the James Ross Basin. The oldest angiospermous leaves are contained within a later Albian flora from Alexander Island, along with conifers, cycads, ferns, ginkgos and bryophytes. The later Albian-Campanian floras from the James Ross Basin show the same elements with rare Ephedrales, but the palynofloras reveal an increasing abundance and diversity of angiosperms. Cenomanian-early Campanian fossil wood from the South Shetland Islands suggests that angiosperms were no longer just understorey trees, shrubs and herbs, but that some were large trees. There has, however, only been a preliminary report on the leaf flora. The Santonian-Maastrichtian saw growing numbers of flowering plants on the Antarctic Peninsula, comprising high proportions of palynological samples and dominating leaf floras in the South Shetland Islands. In the James Ross Basin, Campanian-Maastrichtian wood and spore and pollen assemblages are dominated by podocarps and *Nothofagus*. Angiosperm diversity continued to increase, and while some angiosperms used Antarctica as a migration route between Australia and South America, by the end of the Cretaceous the origins of many taxa lay within Antarctica. By the Paleocene, angiosperms had become dominant. A decreasing diversity and rise to dominance of *Nothofagus* through the Tertiary has been associated with falling temperatures, with Oligocene-Miocene strata in the South Shetland Islands preserving the youngest flora on the Antarctic Peninsula.

Information on the composition of Antarctic Peninsula floras from the Coniacian-Santonian is scarce and very few Late Cretaceous leaf floras have been documented. This study provides new data for an important period in the history of the Antarctic vegetation, when angiosperms were diversifying and increasing in abundance. In Chapter 5, Coniacian-Santonian angiosperm leaf morphotypes are described and their possible botanical affinities are discussed. These results are compiled with previously published reports of angiospermous fossils in Chapter 7 in order to construct a picture of the changing composition of the Antarctic vegetation during the Cretaceous.

1.4 The Cretaceous Antarctic Palaeoclimate

Although the Antarctic Peninsula now has a glacial climate, with mean annual temperatures (MAT) of -3 to -6°C, throughout the Cretaceous and early Tertiary very favourable warm to cool temperate seasonal climates with heavy rainfall allowed extensive forests to flourish (Francis 1986, 1990, Cantrill 1998). The palaeoclimate for the Cretaceous Antarctic Peninsula has been studied using a variety of sources, including plants (e.g. Jefferson 1982a, 1983, Francis 1986, 1999, Rees and Smellie 1989, Askin 1992, Cao 1992, Zastawniak 1994, Cantrill 1998), sedimentary and geochemical information (e.g. Dingle and Lavelle 1998), and marine oxygen isotopes (e.g. Pirrie and Marshall 1990). Plant data has provided independent estimates of temperatures and precipitation on land, deduced mainly from the Nearest Living Relative (NLR) approach (e.g. Cantrill 1998) and tree ring analysis (e.g. Jefferson 1982a, Francis 1986, 1991). Rare palaeoclimate estimates have been proposed based on studies of fossil angiosperm leaf margins and size (Rees and Smellie 1989, Zastawniak 1994). However, previously studied Antarctic angiosperm leaf collections are too small and poorly preserved for the application of modern techniques to determine climate parameters from leaf physiognomy.

Towards the end of the Early Cretaceous, palaeobotanical data indicates that conditions were temperate and humid (Askin 1989a, Cantrill 1998, Francis 1999). NLR methods applied to fern foliage recovered from Aptian sediments on Snow Island suggest mean annual temperatures of at least 8°C (Cantrill 1998). A period of warming began on the Antarctic Peninsula in the Albian, with the widespread occurrence of *Hausmannia* on Alexander Island indicating a climate with a MAT of 13-27°C with monsoonal storms and high seasonal rainfall (Cantrill 1995). Moist warm temperate conditions and a long growing season were also suggested by Jefferson (1982a, 1983) on the basis of tree ring analysis and the presence of large leafed ferns and cycads unable to survive frosts in the Albian forest remains preserved on Alexander Island.

There is only rather limited palaeobotanical data for palaeoclimatic interpretation of the early part of the Late Cretaceous. James Ross Island Albian-Cenomanian podocarp and araucarian conifer and fern palynological assemblages with low proportions of *Classopollis* (the pollen of cheirolepidiaceous conifers common in arid regions) are rain forest associations (Dettmann and Thomson 1987). Based on leaf margin analysis and small leaf size within an angiosperm flora of only six taxa, Rees and Smellie (1989) suggested a MAT of 13-20°C for the Cenomanian-Campanian strata of Williams Point, Livingston Island (Figure 1.1). The spores and pollen present in Turonian-Campanian sediments of the Antarctic Peninsula, including representatives of ferns, podocarps, araucarians, Chloranthaceae, Nothofagaceae, Myrtaceae and Proteaceae, are suggestive of equable, humid or perhumid, temperate conditions (Dettmann 1989). The conifer *Lagarostrobus*, whose modern species are restricted to wet, cool temperate maritime regions, originated in the Turonian and was a dominant element of floras through the Late Cretaceous and into the Paleocene (Askin and Spicer 1992). However, although leaf margins were not preserved in the majority of leaves studied by Zastawniak (1994) from the Santonian-Maastrichtian of King George Island, low leaf size indices were used to infer a subhumid

mesothermal climate. Birkenmajer and Zastawniak (1989a,b) considered the climate of this interval to be generally warm and dry, with summer and winter seasons, and ice only appearing on the tops of higher volcanoes. The suggestion that there was low water availability restricting the growth of extensive vegetation is at variance with other palaeoclimatic studies of the Late Cretaceous Antarctic Peninsula. Dutra (1998) and Dutra *et al.* (1998) interpreted the composition of the Campanian-Maastrichtian floras of King George Island and Nelson Island as indicative of a wet meso-microthermal climate with a season of low humidity. Using the NLR approach applied to Campanian-Maastrichtian floras from King George Island including fungi, ferns and angiosperms such as the climbing lianas of the Loranthaceae, a picture of luxuriant vegetation growing under warm and humid conditions was constructed (Cao 1992, 1994, Zhou and Li 1994). Palynological assemblages from the Campanian-Paleocene of Seymour Island containing Bombacaceae, Olacaceae, Proteaceae and Sapindaceae were considered to reflect high humidity rather than high temperatures and conditions that were warm or mild (Askin 1989a). Plant cuticles have produced estimates of MAT of 8-15°C and mean annual ranges in temperature of 16°C for the latest Maastrichtian of Seymour Island (Askin 1992).

Palaeobotanical evidence points to cooling towards the close of the Cretaceous period. The narrowing of growth rings in fossil wood from the Maastrichtian-Paleocene of Seymour Island and The Naze suggested to Francis (1986, 1991) that the climate was cool, or possibly warm temperate, but low temperatures during the growing season inhibited growth. There is no evidence of a particularly traumatic event at the Cretaceous-Tertiary boundary on the Antarctic Peninsula (Askin 1989a, Francis 1991, Askin 1992). By analogy with modern South American temperate rain forests, Birkenmajer and Zastawniak (1986, 1989a) suggested cool temperate conditions for probable Paleocene floras of King George Island, with a MAT of 10-13°C and annual rainfall of 1000-4000mm and in the late Paleocene-Eocene there is evidence of a warming trend (Francis 1999). The Eocene glaciation proposed by Birkenmajer and Zastawniak (1989b) is suggested to have been restricted to high altitudes (Francis 1999). Wide growth rings in fossil wood (Francis 1996), leaf physiognomy, and warmth-adapted vegetation, e.g. Proteaceae, Myrtaceae, Melastomataceae and Anacardiaceae, reflect a warm or cool temperate climate that was humid but drier than during the Cretaceous (Dusén 1908, Thomson and Burn 1977, Birkenmajer and Zastawniak 1989b, Cao 1992, Li 1994, Dutra 1998). The proliferation of *Nothofagus* in the mid-late Eocene is considered to represent a more seasonal climate, with a pronounced dry season, or falling temperatures (Askin 1992). A sequence of glacial and interglacial periods was reported for the Oligocene (Birkenmajer and Zastawniak 1989a,b), but there are difficulties in the dating of these sediments (Francis 1999). A reduction in diversity during the Oligocene is consistent with a cooling trend (Askin 1992) and the separation of Antarctica from South America and the development of circum-Antarctic ocean currents in the mid-Oligocene caused profound changes in the climate of Antarctica (Birkenmajer and Zastawniak 1989a, Wilford and Brown 1994). The youngest fossil flora known from the Antarctic Peninsula is from the Oligocene-Miocene boundary. This *Nothofagus*-podocarp assemblage with a high proportion of small toothed margined leaves has been compared to moist, cool temperate forests with MATs of 5-8°C and 600-4300mm annual rainfall

(Birkenmajer and Zastawniak 1989a). Although there have been controversial reports of fossils of Pliocene *Nothofagus* communities in the Transantarctic Mountains of East Antarctica (Hill *et al*. 1996), the isolation of the Antarctic continent and the accumulation of ice cover impeded the survival of extensive vegetation.

Additional information on terrestrial palaeotemperatures in the James Ross Basin comes from geochemical indices that reflect degrees of weathering and maturation in Late Cretaceous sedimentary rocks (Dingle and Lavelle 1998), although this approach is reliant on palaeobotanical data to distinguish between the roles of temperature and humidity. Dingle and Lavelle (1998) suggested that peak warmth occurred in the Santonian-Campanian (during the deposition of the Santa Marta Formation). Marine oxygen isotope data from the James Ross Basin were considered indicative of cool temperate climates but also show warming through the Cretaceous with analysis of oysters giving maximum mean temperatures (18.5°C) in the Coniacian-early Santonian (Hidden Lake Formation). In the Santonian-Campanian (Santa Marta Formation) ammonites give a mean temperature of 19.2°C, and belemnites 13.5°C (Pirrie and Marshall 1990, Marshall *et al*. 1993, Ditchfield *et al*. 1994).

1.4.1 Summary

Palaeobotanical data currently available from the Antarctic Peninsula suggests warming through the Cretaceous until the Maastrichtian, when temperatures dropped and remained low during the early Paleocene. The Eocene was another period of warmth, but the latest Eocene-Oligocene saw the onset of the cold conditions experienced today, with only minor recoveries during the Oligocene-Miocene allowing vegetation to return to the Antarctic Peninsula. More research is needed because the NLR methods upon which much of the terrestrial Late Cretaceous climatic interpretations are based are unreliable and because more accurate dating is required. This study of angiosperm leaf floras provides new information on the timing and degree of warmth in the southern high latitudes during the Late Cretaceous greenhouse phase. Palaeoclimatic interpretations from the angiosperm leaf floras studied here are considered in Chapter 6 and this data is discussed in Chapter 7.

2   Preservation of fossil material and methods of study

2.1 Introduction

This chapter aims to illustrate the nature of the Late Cretaceous fossil assemblages studied. There is an explanation of the specimen numbering system, the number of fossil specimens studied for each flora and the methods used to record the data. There then follows an appraisal of the preservation and fragmentation of the Hidden Lake Formation and Santa Marta Formation floras. In Chapter 7 there is a discussion of the taphonomic biases which may have operated on these fossil assemblages and a summary of their implications for this research on floral composition and palaeoenvironment.

Late Cretaceous angiosperm leaf floras from James Ross Island were selected for analysis because they have never previously been studied and they provide new information on Late Cretaceous Antarctic angiosperm flora composition and palaeoclimate. There was a large collection of material available at the British Antarctic Survey, Cambridge, where all specimens mentioned in this study are stored. A list of specimen numbers is given in Appendix 2, Table A2-1 and A2-2. The fossils examined in this study were collected from a total of 15 localities within northwestern James Ross Island (Figure 1.2) and details of each site are given in Table 1.1. The fossils were collected by various geologists and palaeontologists, named in Table 1.1, but in all the collections, even scrappy leaf material was kept. Of the 15 localities, D8754 is from within the Hidden Lake Formation (see Section 1.2.4.1.1). The rest of the localities are within the Santa Marta Formation (see Section 1.2.4.2.1). Throughout this thesis, the Hidden Lake Formation and Santa Marta Formation are frequently abbreviated to HLF and SMF, respectively.

Plate 2.1

1A.   D8754.8.4. Hidden Lake Formation flora.
       Scale bar 10cm.

1B.   D8754.8.30a. Hidden Lake Formation flora. Morphotype 20.
       Scale bar 10mm.

1C.   D8754.8.9a. Hidden Lake Formation flora. Morphotype 25.
       Scale bar 2.5mm.

2.2 Numbering of specimens

All British Antarctic Survey specimens are numbered with a consistent BAS scheme. The first letter, i.e. D or DJ, refers to the locality. Then a three or four figure number refers to a particular sublocality, e.g. DJ147. Only the locality D8754.8 has another number after a period that refers to a particular horizon within a log at that locality. The next number following a period refers to the rock sample, e.g. DJ147.46 or D8754.8.16. Part and counterpart are sometimes referred to using the same number and A or B, e.g. DJ134.15A&15B, but this is not always the case because difficulty in immediately recognising part and counterpart has sometimes led to them being given different numbers, e.g. D8754.8.6&65. In some cases the samples are broken up and may have therefore been previously referred to as A, B or C. Where these have been glued together to reassemble a specimen, this is indicated with a forward slash, e.g. D8604.37A/C with a counterpart D8604.37B. There may be several leaf specimens on one slab and these are referred to with a lower case letter, e.g. D8754.8.4a and D8754.8.4c refers to two different leaf specimens on slab D8754.8.4. Samples from the Hidden Lake Formation flora all begin with D8754.8 and the samples from the Santa Marta Formation flora include numbers D8604, D8605, D8606, D8609, D8610, D8616, D8618, D8619, D8621, D8625, DJ134, DJ147, DJ451, and DJ452.

2.3 Specimen information

2.3.1 Hidden Lake Formation flora

The Hidden Lake Formation flora from locality D8754.8 comprises a collection of 101 rock slabs. A total of 145 macrofossils have been drawn and examined. Of these, 93 are dicotyledonous angiosperm leaf specimens. A further ten fragmentary angiosperm leaf specimens were described from photographs only. For nine of the angiosperm leaves, the part and counterpart are preserved. Thus, in total, 94 individual dicotyledonous angiosperm leaves were studied. The rest of the flora is made up of ferns (41 specimens - two are counterparts), bennettites (three specimens – one is a counterpart), one conifer specimen, and seven poorly preserved specimens of unknown affinity. The composition of the collection is illustrated in Figure 2.1.
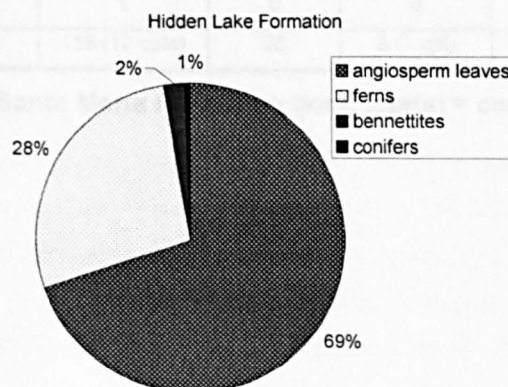
Figure 2.1 Summary of the composition of the Hidden Lake Formation fossil assemblage.

The scattered leaf fossils (Plates 2.1A, 2.2D) are preserved as impressions with brown carbonaceous residues within rusty-brown, burrowed sandy siltstones. Although there is no cuticle present, in general the preservation of the leaves is very good. The architectural features of the leaves, such as leaf form, margins, and venation patterns of the primary, secondary, tertiary and occasionally higher orders, are clearly visible in most specimens. The rock surfaces on which these leaf fossils are preserved are often very curved.

2.3.2 Santa Marta Formation flora

Within the Santa Marta Formation flora, a total of 176 fossils preserved on 175 rock slabs were examined (see Table 2.1). There are 118 dicotyledonous angiosperm leaf specimens and for 19 of the angiosperm leaves the part and counterpart are preserved, making the total number of individual angiosperm leaves studied 99. There are also ferns (25 specimens), bennettites (two specimens – one is a counterpart), conifers (13 specimens – three are counterparts), seeds (nine specimens), and nine poorly preserved specimens of unknown affinity. The composition of the Santa Marta Formation collection is illustrated in Figure 2.2.

Locality	Number of slabs	Number of specimens	Angiosperm leaves	Ferns	Bennettites	Conifers	Seeds	Unknown
D8604	6	6	6 (2 cpts)	0	0	0	0	0
D8605	38	41	24 (5 cpts)	7	0	1	0	9
D8606	8	8	7 (2 cpts)	1	0	0	0	0
D8609	4	3	1	0	0	2	0	0
D8610	2	2	2 (1 cpts)	0	0	0	0	0
D8615	2	2	0	0	0	2 (1 cpt)	0	0
D8616	2	2	2	0	0	0	0	0
D8617	2	0	0	0	0	0	0	0
D8618	1	1	1	0	0	0	0	0
D8619	4	4	4	0	0	0	0	0
D8621	1	1	1	0	0	0	0	0
D8625	1	1	1	0	0	0	0	0
DJ134	37	38	14 (3 cpts)	5	2 (1 cpt)	8 (2 cpts)	9	0
DJ147	65	65	53 (6 cpts)	12 (1 cpt)	0	0	0	0
DJ451	1	1	1	0	0	0	0	0
DJ452	1	1	1	0	0	0	0	0
Totals	175	176	118 (19 cpts)	25	2 (1 cpt)	13 (3 cpts)	9	9

Table 2.1 The Santa Marta Formation flora, (cpt(s) = counterpart(s)).

Santa Marta Formation

5%

8%

1%

15%

71%

- ▨ angiosperm leaves
- ▢ ferns
- ▉ bennettites
- ▉ conifers
- ▥ seeds
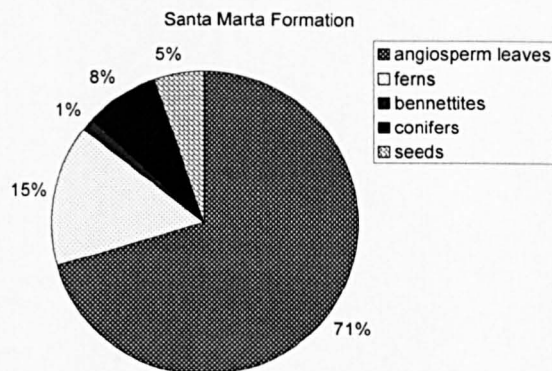
Figure 2.2 Summary of the composition of the Santa Marta Formation flora.

There are a variety of preservation styles within the Santa Marta Formation flora. The angiosperm leaves are preserved as true impressions (Plate 3.8A), impressions with carbonaceous residues (Plate 2.2B), cream-coloured calcareous permineralisations (Plate 2.2A and 2.2C), or as combinations of all these types, within grey, fine-grained silty sandstones or mudstones and calcareous concretions. The preservational style of each specimen is presented in Appendix 2, Table A2-1 and A2-2. It was confirmed that the permineralised fossils were calcareous by observing the reaction when dilute hydrochloric acid was applied.

2.4 Methods

2.4.1 Macrofossil preparation

Broken up specimens were pieced together and fixed in place using wood glue or two part epoxy resin. Parts of many of the impression fossils were obscured by sediment cover or secondary mineralisation. Attempts were made to remove sediment by hand using a small diameter chisel but this was not possible for the very hard quartz-rich sediment. In some cases it was possible to reveal more of the leaves using an air abrasive drill (e.g. D8754.8.30a, Plate 2.1B, Appendix Volume 2 p19, 87, 88). However, the high curvature of the surfaces of the sediments meant that there was sometimes a great thickness of sediment to be removed and this was not always possible without causing much damage to the specimen.

Specimens of the Santa Marta Formation flora, which are preserved in calcareous concretions, were sometimes obscured by secondary calcareous mineralisation. Whether the fossil leaves were preserved as true impressions, impressions with carbonaceous film, or impressions with calcareous permineralisation, attempting to dissolve secondary calcareous mineralisation with HCl was considered too destructive. Instead it was possible to gradually lift off the secondary calcareous mineralisation or adhering sediment by hand using a scalpel or small chisel (e.g. DJ147.46a, Appendix Volume 2 p191, 309). This work was generally carried out under a stereo microscope. Very gently pressing on the covering material at an oblique angle and applying water was found to make separation easier. Small brushes were also useful for removing loose sediment.

Plate 2.2

2A.   DJ451.7a. Santa Marta Formation flora. Morphotype 16.
       Scale bar 5mm.

2B.   DJ147.6a. Santa Marta Formation flora. Morphotype 29.
       Scale bar 5mm.

2C.   D8604.54a. Santa Marta Formation flora. Morphotype 13.
       Scale bar 2.5mm.

2D.   D8754.8.27a. Hidden Lake Formation flora. Morphotype 2.
       Scale bar 2.5mm.
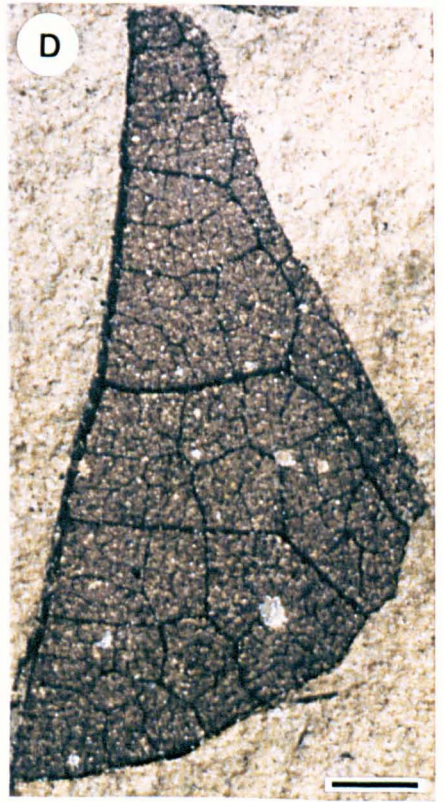
2.4.2 Photography and drawing

Earliest attempts in this project to describe these fossils were made using black and white photographs taken in the Biology Department, University of Leeds. Low magnification photographs of the rock slabs were taken with a macro lens and higher magnification photographs of the leaves were obtained using a Zeiss Tessova and fibre optic lighting. High magnification photographs were also taken with an Olympus SZH10 Research Stereo Microscope and a camera attachment.

Ethanol was applied to some of the leaf specimens to increase contrast. Although this makes the morphology of the leaf specimens much clearer, it causes problems with reflections of light, the end result being white patches on the prints. To reduce the problem of reflectance when ethanol was applied to the fossil leaves, attempts were made to photograph specimens completely submerged in a bath of ethanol. Although the reflectance problem was overcome, it was far outweighed by the resulting loss of contrast in the photographs.

To obtain a clear reproduction of the leaf architecture, it was attempted to trace features such as margins and venation patterns from these photographs on to acetate overlays. However, the surfaces of most of these leaf fossils are very uneven, making it impossible to get the entire specimen in focus during photography. Even with the specimen and a stereo microscope to hand, this was a very time consuming and difficult task.

The most successful approach proved to be reproducing and describing the leaf architecture using drawings made with an Olympus SZH10 Research Stereo Microscope and a drawing tube attachment. These drawings were made at the British Antarctic Survey, Cambridge, and in the Department of Biology and the School of Earth Sciences at Leeds University. The eyepiece used was 10x and a variety of objectives were used, 0.5, 1.0 and 1.5x.

To increase contrast and make the features of the fossils clearer, drops of ethanol were applied to the surfaces of specimens. This was particularly useful for the leaves preserved as brown carbonaceous films. These specimens were drawn and photographed using high angled fibre optic lighting. For many of the impressions and permineralisations, the addition of ethanol was not necessary and the fossils were drawn dry, lit with low angle lighting from various directions. Many of the permineralisations and impressions were, however, clearer with high angle lighting and/or ethanol applied. The fine detail of particular features in the best preserved leaves, e.g. marginal teeth and high order venation, were redrawn at higher magnifications.

Many of the leaves were drawn more than once. It was frequently necessary to draw the specimens with alcohol applied and dry using lighting from several different directions. This revealed much more of the fossil morphology and also helped to ensure that the features drawn were actually veins and part of the leaf architecture rather than preservational features. The surfaces of some of the specimens were so uneven that it was necessary to draw the

specimens more than once with the slabs tilted at different angles. The rock surfaces on which some of the specimens are preserved are so uneven that there may unavoidably be distortion in the drawings and these leaves are recorded in Appendix 2, Table A2-1 and A2-2.

Where the part and counterpart are preserved, both were drawn and studied. This is obviously beneficial in cases were the part and counterpart preserve different parts of the leaf, as in D8754.8.62a and D8754.8.64a (Morphotype 32, Figure 5.21) and DJ147.49Aa and DJ147.49Ba (Morphotype 37, Figure 5.22). Using a graphics package it was possible to superimpose part and counterpart to make a composite drawing to facilitate description (Figures 5.21c and 5.22f). Leaf specimens with separated fragments could also be reconstructed using a graphics package (e.g. D8754.8.101a and D8754.8.38a, see Appendix Volume 2 p148, 97).

Another part and counterpart D8754.8.32a and D8754.8.98e (Figure 2.4 and Appendix Volume 2 p21, 90) illustrate the point that the close observation of both can be crucial. D8754.8.32a was drawn and described, but the counterpart D8754.8.98e was not discovered at BAS until much later. The leaf was originally described as almost whole, with the apex and base preserved and an entire margin and possibly acrodromous venation. Detailed observation of D8754.8.98e, however, revealed that the specimen was actually just a small fragment from one side of a much larger leaf. The apex and base of the leaf are not preserved, the venation appears to be pinnate and the margin is actually toothed. This example is also an illustration of how the preservation of many of these leaves makes them very difficult to describe and why it was necessary to make drawings from detailed microscope observation.
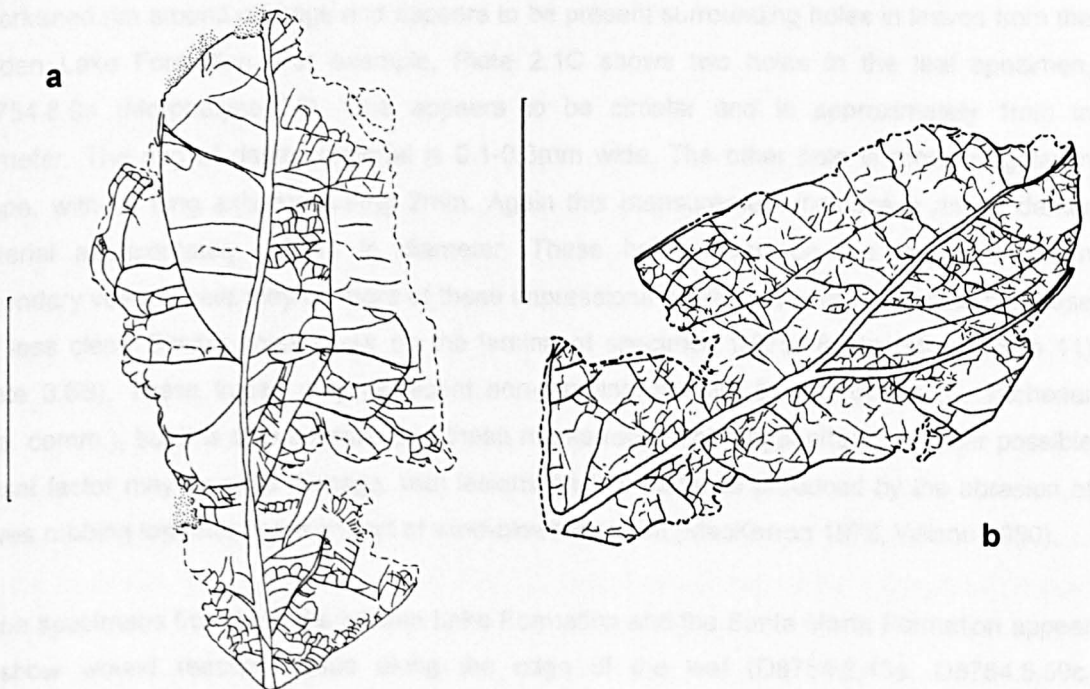
Figure 2.3 (a) D8754.8.32a. (b) D8754.8.98e. Part and counterpart. Scale bar is 10mm.

It is clear that not every line on the drawings is a representation of leaf venation, but features of the true venation pattern could then be interpreted from each drawing. The photographs were useful in helping to decide which features were true veins. The different vein orders distinguished were marked on each drawing in different colours (see Figure 3.1 and Appendix Volume 2).

These drawings were then scanned into computer and measurements, e.g. leaf area, were made using image analysis software (ImageJ). These drawings and photographs then form the basis for the isolation and description of dicotyledonous angiosperm leaf taxa. These are described in the following chapters.

2.4.3 Replication

Studied under a light microscope, there is no relief visible in the Hidden Lake Formation leaf fossils. In an attempt to obtain information on the characteristics of the leaf surfaces, replicas were made using latex and cellulose acetate film with acetone. The results were examined using light microscopy and also scanning electron microscopy but the lithology is rather coarse grained and no leaf details were visible.

2.5 Preservation of leaves

2.5.1 Pre-abscission leaf damage

There is some evidence of damage to the leaves probably occurring while they were still growing on the plant. This is recognised by the presence of wound reaction tissue, which only forms on living plant material (Scott and Titchener 1999). Wound reaction tissue is identified as a darkened rim around damage and appears to be present surrounding holes in leaves from the Hidden Lake Formation. For example, Plate 2.1C shows two holes in the leaf specimen, D8754.8.9a (Morphotype 25). One appears to be circular and is approximately 1mm in diameter. The ring of darker material is 0.1-0.3mm wide. The other hole is more irregular in shape, with its long axis measuring 2mm. Again this measurement includes a rim of darker material approximately 0.2mm in diameter. These holes occur on the lamina between secondary veins. There may be more of these impressions distributed over the lamina but these are less clear. Similar holes occur on the lamina of specimen D8754.8.54a (Morphotype 11) (Plate 3.6B). These traces may represent non-marginal feeding by arthropods (F. Titchener pers. comm.), but it is also possible that these marks represent fungal attack. Another possible causal factor may be wind damage, with lesions on leaf surfaces produced by the abrasion of leaves rubbing together or the impact of wind-blown material (MacKerron 1976, Wilson 1980).

Some specimens from both the Hidden Lake Formation and the Santa Marta Formation appear to show wound reaction tissue along the edge of the leaf (D8754.8.43a, D8754.8.59c, D8754.8.60a, DJ147.25a). For example, the apex of D8754.8.43a (Morphotype 36, Plate 3.4D)

is missing and along this broken edge there is a darker rim. This may possibly represent tip feeding or wind damage.

Galls are abnormal morphological structures of plants induced by other organisms causing reactive growth of the plant tissues (Diéguez *et al.* 1996). For example, mites, midges or wasps living or growing on leaves may produce galls. The holes present in D8754.8.1a (Plate 3.4A) may represent gall abscission or blotch mines (F. Titchener pers. comm., M. Collinson pers. comm.). The largest of these holes measures 7.2mm by 2.9mm and is positioned at the junction of the basal lateral primary vein and the midvein. There are also several other holes (with long axes ranging from 1.3-2.5mm) distributed over the lamina, predominantly adjacent to secondary veins. In some of the leaves from the Santa Marta Formation there are spherical objects on the laminae that may represent leaf galling (e.g. DJ147.49Aa&Ba, D8605.31a). For example, on the lamina of specimen D8605.31a (see Appendix Volume 2 p158, 229) there is a 'segmented doughnut' shaped object, approximately 1.4mm in diameter, with a central hole approximately 0.4mm in diameter. Only one is observed in this fragmentary leaf and it occurs in between two secondary veins. A similar object, with a diameter of 0.7mm and an inner hole 0.2mm across, is observed on the lamina of DJ147.49Aa&Ba (Morphotype 37, Figure 5.22d,e).

This possible evidence of plant-insect interaction demonstrates that these angiosperm leaves may have provided a food resource for arthropods in Antarctica during the Late Cretaceous. The recognition of coevolutionary relationships between plants and animals existing during the Cretaceous is important to researchers creating models for determining palaeoclimatic parameters from foliar physiognomy. For example, the character scoring method used in CLAMP analysis for determining palaeoclimate considers a spiny margin to be entire, based on the assumption that these are more related to the deterrence of herbivory than climate (Wolfe 1993).

2.5.2 Fragmentation

The details of preservation of the 103 Hidden Lake Formation angiosperm specimens and 118 Santa Marta Formation specimens are presented in Appendix 2, Table A2-1 and A2-2. This data is summarised below. Figure 2.4 summarises the completeness of the leaf fossils from both floras. Leaves categorised as 'almost whole' have only a very small part of the leaf missing, such as the tip of the apex or a small part of the margin. The shape of these leaves can generally be easily interpreted from the curvature of the margins present. Approximately 25% of the leaves of both floras are almost whole. The leaves assigned to the 'fragment' category preserve quite a large proportion of the leaf such that although the base or apex of the leaf may be incomplete, there are clear margins preserved and many architectural features can still be observed. 'Small fragment' does not refer to the actual size of the specimen, but is an indication that only a small proportion of the original leaf has been preserved. In these leaves, there is either only a very small percentage of the margin remaining (less than 20%) or no margins at all. The shape of these leaves cannot, therefore, be determined.
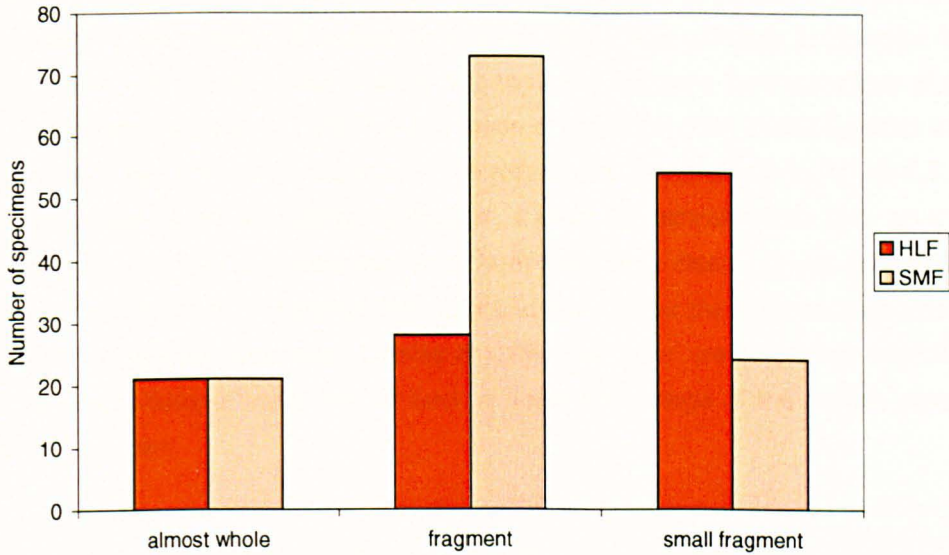
Figure 2.4 Degree of fragmentation of the leaf fossils from the Hidden Lake Formation and Santa Marta Formation floras.

The clarity of the venation within the leaves from both floras is summarised in Figure 2.5. These subjective terms were assigned based on the number of vein orders present in the fossil leaf. Vein orders include primary, secondary, tertiary, quaternary, or quinternary veins, and marginal ultimate venation or tooth venation. Vein orders are explained in Chapter 3 and Appendix 1. Each venation category is explained in Table 2.2.

Venation	Number of vein orders present
Very clear	At least 5
Clear	4
Fairly clear	3
Fairly unclear	2
Unclear	1

Table 2.2 Definition of venation categories used in the assessment of leaf preservation in this study.
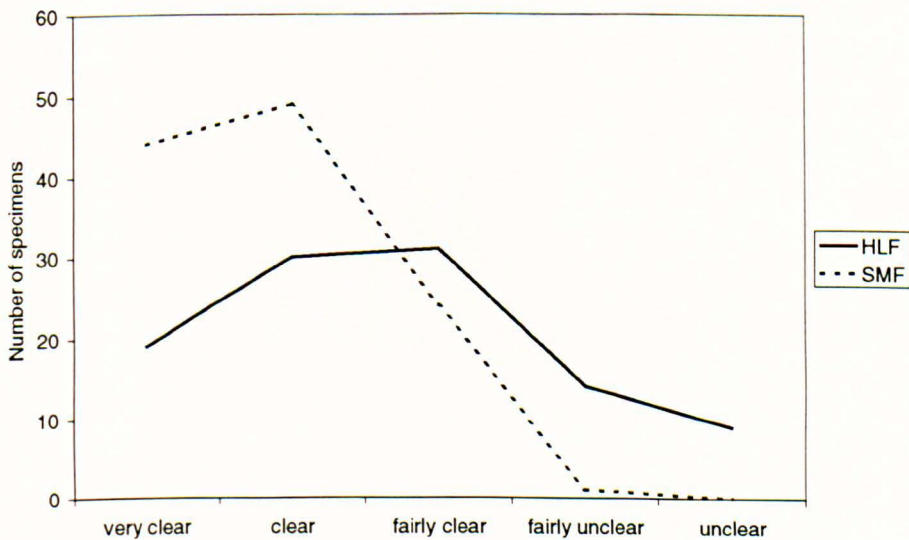
Figure 2.5 Preservation of venation within the leaf fossils from the Hidden Lake Formation and the Santa Marta Formation floras.

All the leaves from both floras were given a rating from very poor to excellent. These ratings are an assessment of the number of architectural characters it was possible to describe for each specimen. These ratings were calculated by scoring the specimens by the number of features present. This scoring is given in Table 2.3 and these scores were then added together and used to rate each leaf specimen, see Table 2.4. The results are summarised in Figure 2.6. So, for example, for a leaf to be considered 'excellent', it must be almost whole and have a clear margin, an apex and base and venation which is at least fairly clear. Leaves considered 'very good' may be almost whole or fragmentary, but must have either the base or apex present and venation which is at least fairly clear. Leaves described as 'poor' are only small fragments with both the apex and base missing and, at best, a small percentage of the margin present and fairly unclear venation.

Feature	Scoring
Degree of fragmentation	Almost whole – 3, Fragment – 2, Small fragment – 1
Clarity of venation	Very clear – 5, Clear – 4, Fairly clear – 3, Fairly unclear – 2, Unclear – 1
Margin	Clear – 2, Small percentage – 1, None – 0
Apex	Complete – 2, Incomplete – 1, Missing – 0
Base	Complete – 2, Incomplete – 1, Missing – 0
Both apex and base present	Yes – 1, No – 0

Table 2.3 Scoring system used to rate preservation of leaf specimens.

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

Table 2.4 Ratings used in the description of leaf preservation.
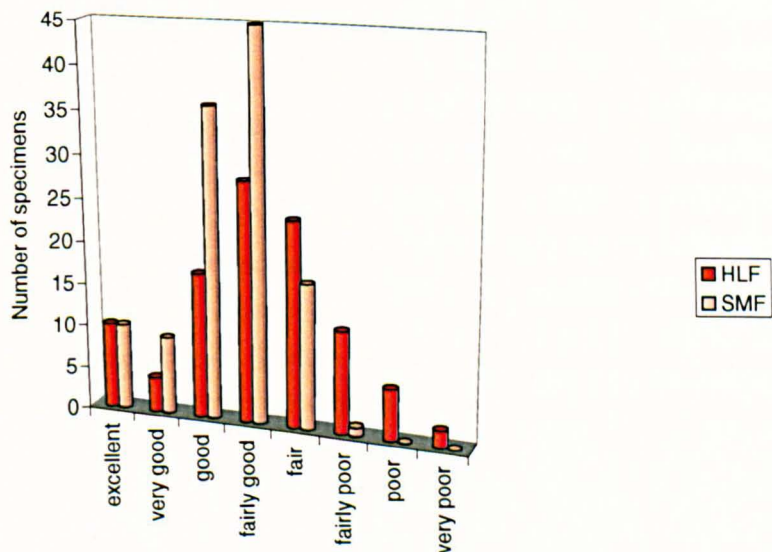
Figure 2.6 Preservation of leaf specimens from the Hidden Lake Formation and Santa Marta Formation floras using ratings defined in Table 2.3 and Table 2.4.
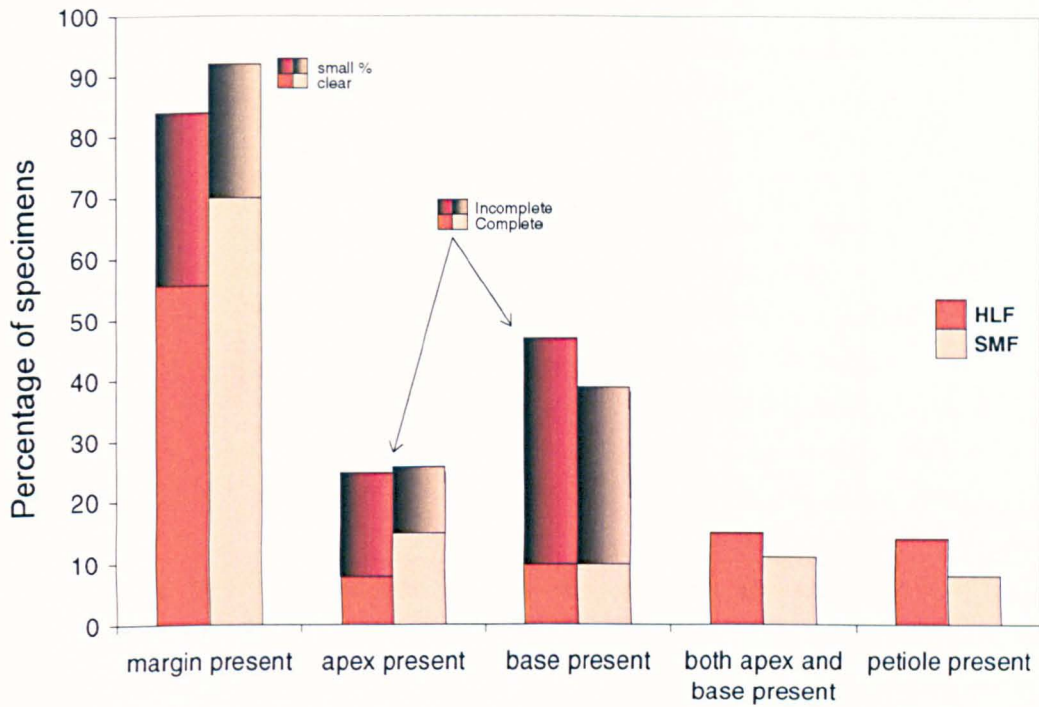
Figure 2.7 The completeness of the leaf specimens from the Hidden Lake Formation and Santa Marta Formation floras.

From Figure 2.7 it is clear that the leaf margins are preserved in the majority of the specimens. The bases are preserved in almost half the leaves and in 20-30% of leaves with bases, the petiole is also preserved. Some of the leaves have both the apex and base preserved, but the apices of the leaves are the parts that are most frequently missing, present in approximately 25% of the leaves of each flora.

2.5.3 Leaf size

Specimen measurements of length, width and area are given in Appendix 2, Table A2-3 and A2-4. Figure 2.8 presents the measurements of leaf length and width for the Hidden Lake Formation and Santa Marta Formation floras. The maximum length of each specimen was measured parallel to the midvein and the maximum width was measured perpendicular to the midvein. The actual size of each specimen is indicated in blue in Figure 2.8. Where present, these length measurements included the petiole. For the Hidden Lake Formation flora, the maximum specimen length ranges from 5-72mm (average 30mm) and the maximum specimen width ranges from 4-45mm (average 19mm). For the Santa Marta Formation flora, the maximum length ranges from 5-95mm (average 32mm) and the maximum width from 6-70mm (average 19mm).
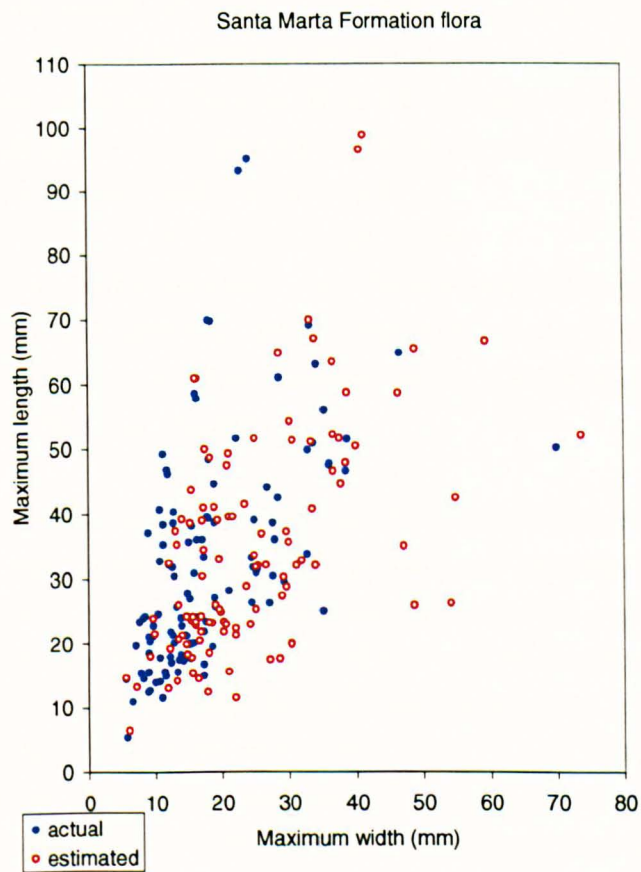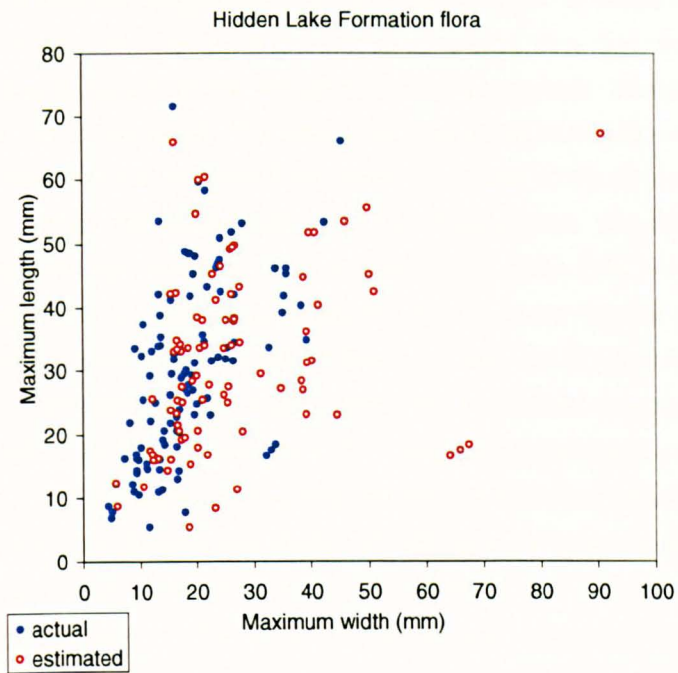
Figure 2.8 Length and width measurements for the Hidden Lake and Santa Marta Formation floras.

The actual measurements refer to the size of the specimen, including the petiole, while the estimated measurements refer to the minimum size of the lamina, excluding the petiole.

Since many of the leaves are fragmentary, a significant number of these measurements are minimum estimates of maximum length and width so estimates were then made by filling in the leaf margins using the curvature of the margins present as a guide. These estimated lamina lengths are shown in red in Figure 2.8. The petiole was excluded and these measurements refer to the length of the lamina alone. In many of the leaves one side of the lamina is more complete than the other, so, under the assumption that the leaves were roughly symmetrical, the maximum width estimate was obtained from the most complete side and doubled. For the Hidden Lake Formation flora, this gave estimates of maximum lamina length of 5-67mm (average 31mm) and maximum lamina width of 6-91mm (average 26mm). For the Santa Marta Formation flora, the maximum lamina length ranges from 6-99mm (average 35mm) and the maximum lamina width 6-74mm (average 25mm). These estimates are only a little greater than the actual dimensions of the specimens because the parts added were based on bare minimum outlines and so the estimated lengths and widths are still minimum approximations of the length and width of the original leaf. With evidence of the original shape of the leaf, it is possible to make a better reconstruction of the original outlines and length/width ratios of the leaf fragments. Once leaf fragments have been successfully arranged into taxa, it is then possible to make more accurate estimates of leaf size (see Chapter 6).

Figure 2.9 presents the results of different approaches of measuring the area of these specimens. The actual area of each specimen, again including the petiole, was measured with the aid of image analysis software. The area within the estimated minimum outline, excluding the petiole, was also measured in the same way. A third estimate of lamina area was calculated by applying the following equation cited by Webb (1959):

$$Area = 2/3 \times length \times width$$

The length and width used in this calculation were the estimated maximum lamina length and width. This equation has been used frequently in palaeobotanical studies to obtain estimates of leaf area (e.g. Pole 1993a, Wilf et al. 1998). Estimates of leaf area made using this equation are indicated throughout this thesis as 'leaf area'.

The actual area of the Hidden Lake Formation specimens ranges from 20-1609mm^2 (average 340mm^2), the estimated minimum area from 20-4926mm^2 (average 560mm^2), and the calculated minimum area from 22-4068mm^2 (average 545mm^2). The actual area of the Santa Marta Formation specimens ranges from 21-2030mm^2 (average 402mm^2), the estimated minimum area from 28-3129mm^2 (average 640mm^2), and the calculated minimum area from 25-2741mm^2 (average 611mm^2). Again the fragmentary nature of most of the specimens means that all these dimensions are minimum estimates for the area of the original leaves. It was concluded that the closest estimates to the assumed true leaf areas were obtained by drawing a minimum leaf outline and measuring the area with the aid of image analysis software. The equation to calculate leaf area from maximum length is based on the shape observed in complete leaves and takes the narrowing of the leaf apex and base into account. Since the majority of these Cretaceous fossil leaves have their apices missing and the leaf length is

frequently unavoidably underestimated, the calculation gives a more reduced estimate of leaf area.

Hidden Lake Formation flora

Santa Marta Formation flora
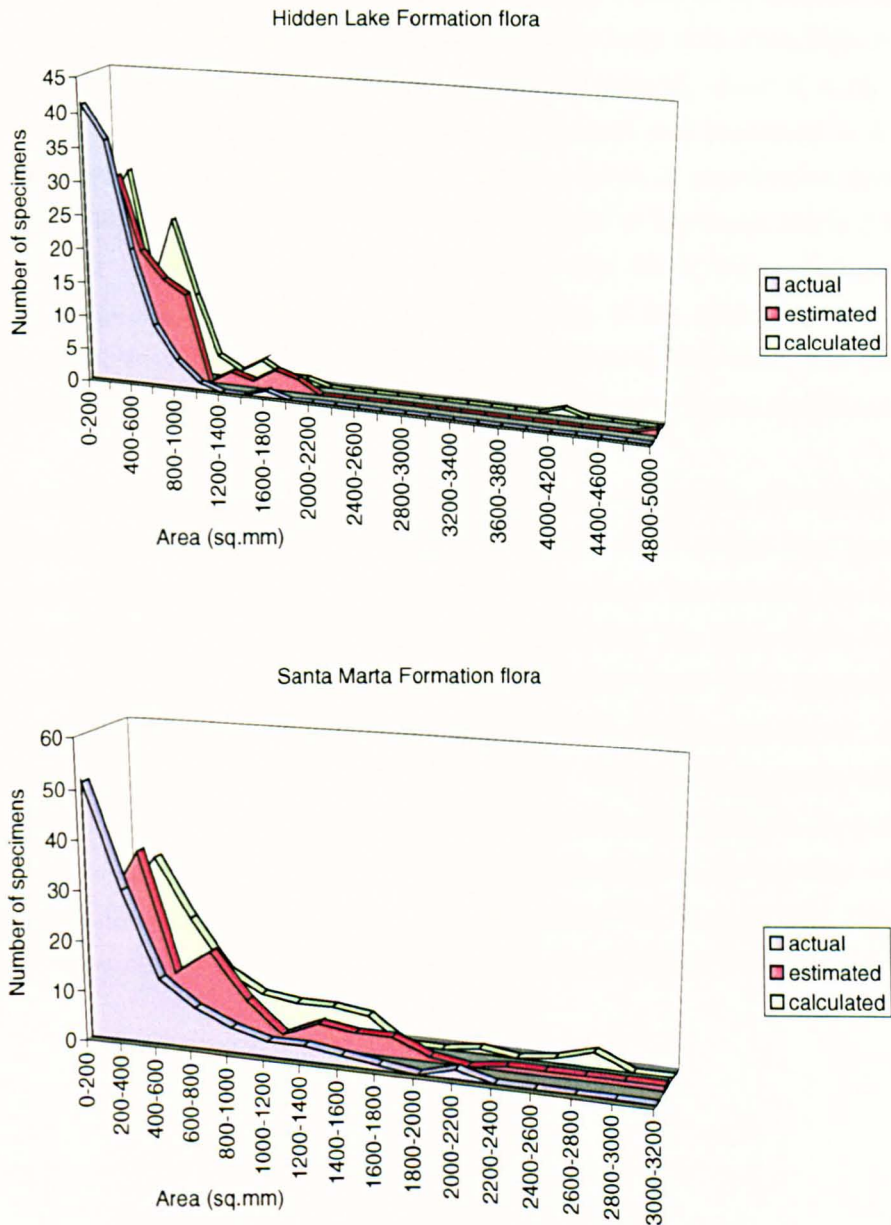
Figure 2.9 Leaf area measurements for the Hidden Lake and Santa Marta Formation floras.

The actual measurements refer to the area of the specimen, including the petiole, while the estimated measurements refer to the minimum area of the lamina, excluding the petiole. The calculated measurements were obtained using the formula above, area = 2/3 x length x width.

2.5.4 Comparison of Hidden Lake Formation and Santa Marta Formation specimens

Although an approximately equal number of leaves were studied from each flora, with the same number of almost complete leaves in each, the two different floras have different qualities. There is a greater proportion of small fragments in the Hidden Lake Formation flora. Although the Santa Marta Formation flora also contains fragmentary material, there is a far smaller proportion of small scrappy fragments. The venation is also less well preserved in a greater proportion of the Hidden Lake Formation leaves. There is a range of preservation levels from poor to excellent in the Hidden Lake Formation flora, but most of the Santa Marta Formation fossils are rated fair to excellent. A greater number of the Santa Marta Formation leaf specimens have clear margins preserved. The average size of the Santa Marta Formation leaves is also greater than the Hidden Lake Formation specimens. Therefore, it is concluded that the Santa Marta Formation flora consists of a greater number of better preserved leaves.

It is clear that the Hidden Lake Formation flora contains a greater proportion of fragmentary and less well preserved specimens. However, this should not be used to infer any taphonomic differences between the two floras because the results presented in this chapter are biased by the fact that I studied the flora from the Hidden Lake Formation first. The Santa Marta Formation flora was the second to be studied and at this stage it was clearer to me which leaves were too fragmentary and poorly preserved to provide useful information. This fact, however, does not affect the results from the palaeoclimate section (Chapter 6). The most fragmentary and poorly preserved small unidentifiable scraps of leaf material from both the Hidden Lake Formation and the Santa Marta Formation that did not provide enough characters to be included within the numerical taxonomic analysis (Chapter 4) could not be grouped into morphotypes. This means that the results from the Hidden Lake Formation and Santa Marta Formation floras are comparable.

3 Approach to leaf descriptions

3.1 Introduction

This chapter outlines the approach used to describe the Cretaceous Antarctic angiosperm leaves in this project. A standardised terminology is required to provide a framework within which critical comparison of detailed architecture of modern or fossil leaves can be made.

The initial stage of this research was to identify which of the leaves actually were dicotyledonous angiosperms. At this level of preservation it is often very difficult to readily select the angiosperms for study without detailed observation of all the available fossil material. Dicotyledonous angiosperm leaves are usually characterised by reticulate or net-like venation, but this is not a consistent or unique feature (Thomas and Spicer 1987). Some pteridosperms (e.g. *Sagenopteris*), gymnosperms (e.g. *Gnetum*), and ferns (e.g. *Hausmannia*) show reticulate venation, superficially appearing similar to angiosperm venation. Angiospermous origin was confirmed by the recognition of at least three distinct vein orders within the fossil leaves (see Section 3.2), which are not apparent in other plant groups (Hickey and Wolfe 1975).

There are many different kinds of features that can be used in classification of fossil dicotyledonous angiosperm leaves. The preservation of these Antarctic leaves does not allow examination of cuticle and anatomical detail because it is not present, but they show clearly the intricate detail of leaf architecture, such as leaf shape, marginal features and venation patterns. The approach used here is based on analysis of these morphological features. There are several schemes providing terminology to aid in the description of dicotyledonous angiosperm leaf architecture (see Section 3.2). A precise descriptive approach is required because superficial matching of leaf types leads to misidentification (Hickey 1973, Dilcher 1974), see Section 3.5. This is especially pertinent in the analysis of this Cretaceous flora with a presumed high proportion of extinct forms.

3.2 Features used in the description of dicotyledonous angiosperm leaf architecture

3.2.1 Hickey's terminology

The importance of leaf architecture in the classification of dicotyledonous angiosperms has been validated by extensive studies of extant leaves (e.g. Hickey and Wolfe 1975, Klucking 1986-1997). Certain combinations of characteristics of size, shape, margins, apex, base, petiole, glands and venation are unique to certain taxa (Dilcher 1974). The features of marginal teeth have been shown to be particularly useful (Hickey and Wolfe 1975). Hickey (1973, 1979) outlined the characters of leaf architecture that he used to classify dicotyledonous angiosperm leaves resulting from an extensive survey of living and Early Cretaceous-Pleistocene fossil specimens. This system is adapted from the earlier schemes of Turrill (published by Stearn

1956), defining shape classes, and von Ettingshausen (1861) (referred to in Hickey 1973), classifying patterns of leaf venation. Hickey's choice of features was also influenced by Lam (1925) (referred to in Hickey 1973), who recognised the taxonomic significance of angular relationships and courses of secondary and tertiary veins, and venation studies by Foster (1950). Hickey (1973) developed this classification to clarify descriptive terminology, eliminating ambiguity, and to produce a coherent system encompassing all aspects of leaf architecture. This scheme allows precise and concise description of dicotyledonous angiosperm leaf elements and Hickey (1977), for example, used it in his report on the early Tertiary floras of western North Dakota.

This scheme is the one most commonly used internationally by palaeobotanists (e.g. Hill 1983, 1986, 1991; Czajkowski and Rösler 1986, Tanai 1986; Crabtree 1987; Crane *et al.* 1988; Hill and Christophel 1988; Birkenmajer and Zastawniak 1989a; Rees and Smellie 1989; Zastawniak 1990, 1994; Upchurch and Dilcher 1990; Pole 1993a; Li 1994; Scriven *et al.* 1995; Cantrill and Nichols 1996; Manchester *et al.* 1998) and is also used in research on modern leaves (e.g. Jones 1986). Also, since Hickey's scheme is a modified version of older schemes, some of these terms have been in use for a long time (e.g. Berry 1916-1945) and are widely recognised by the botanical and palaeobotanical community.

Hickey (1973, 1979) defined a set of terms relating to the orientation, organisation, shape, margin, texture, gland position, petiole, venation pattern, orders of venation, and tooth architecture of dicotyledonous angiosperm leaves. The main features of Hickey's scheme are outlined as an illustrated glossary in Appendix 1. In most dicotyledonous angiosperm leaves the venation can be differentiated into a number of size classes determined by their relative size at their point of origin and also their course and distribution (Figure 3.1).
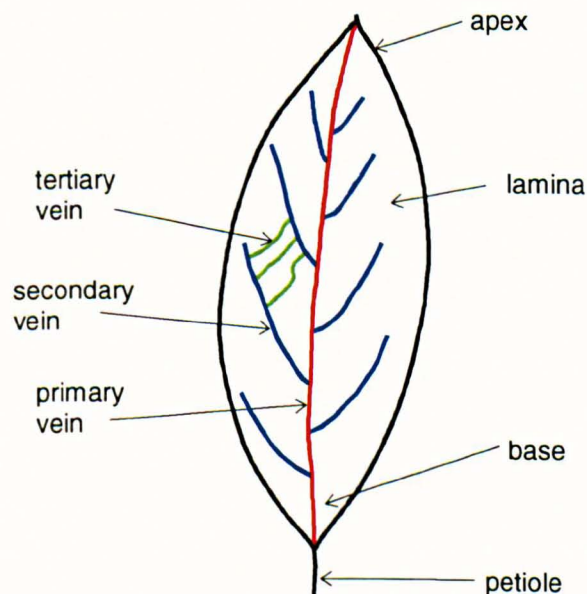
Figure 3.1 The parts of a dicotyledonous angiosperm leaf of importance in this study.

Although it is often difficult, the recognition of vein orders is fundamental to Hickey's classification and the method to recognise each order, which was adopted in this study of Cretaceous leaves, is summarised from Hickey (1979) below:

The primary vein is the thickest occurring either singly as the midvein or as a medial vein accompanied by lateral primaries of roughly equal thickness. These emerge from the petiole and may give rise to additional lateral primary veins above the leaf base. To identify the successive vein orders, veins are traced from their point of origin and the widths of the lateral vein branch and the continuation of the source vein are measured just above the point of branching. Where the lateral vein branch is approximately equal in width to the continuation of the source vein, both branches are of the same order (Figure 3.2a). Where the lateral vein branch is markedly finer than the continuation of its source, that branch is of a higher order (Figure 3.2b). So, the set of markedly smaller branches arising from the primaries are secondary veins, the next finer set arising from the primaries and secondaries are tertiary veins, and so on.
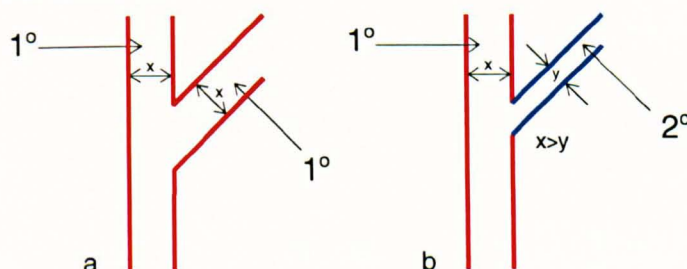
Figure 3.2 Recognition of vein orders; (a) branch of the same order; (b) branch of a higher order.

The relative thickness is, however, variable, so when the boundaries between size classes are not particularly clear, it is then necessary to consider the behaviour of the veins to identify the different orders. For example, slightly thinner secondary vein branches are recognised as secondaries by their geometry (Appendix 1, Figure A-14). These outer secondary veins are a clear feature in specimen D8621.27a (Plate 3.8A, Morphotype 7, see Chapter 5). Intersecondary veins are intermediate in thickness between second and third order veins. These most often originate on the midvein interspersed between and roughly parallel to the secondaries of pinnate leaves (Appendix 1, Figure A-15e), e.g. specimen D8754.8.8a (Figure 3.3a, Plate 3.6A, Morphotype 25, see Chapter 5).

Although Hickey (1973, 1979) proposed divisions between categories for many characters based on clear breaks he observed, he was also aware that there are leaves that fall into transitional zones between character definitions such as apex styles or venation classes. One of the most widely reported difficulties with this scheme is the problem of distinguishing between the imperfect actinodromous venation class and the pinnate venation class where the lowest

pair of secondary veins arises from the primary at a different angle from those above (see below).

3.2.2 Other character lists available for use in the description of angiosperm leaves

There are several other morphologically based character lists for use in the classification of angiosperm leaves:

- Schemes erected earlier than that proposed by Hickey (1973) have not been widely adopted by palaeobotanists working on Cretaceous angiosperm leaves and so have not been assessed.

- Dilcher (1974) developed a character list taking the cuticular features of fossil leaves as well as leaf architecture into account. Details of cuticular anatomy are not preserved within the Cretaceous Antarctic leaf impression fossils studied here, so terminology for cuticular characters was not required. The leaf architectural characters within Dilcher's system are incorporated from Hickey's (1973) scheme with slight modifications to the layout and illustrations, so Dilcher's character list was not further considered.

- Melville (1976) (referred to in Hickey 1979) proposed an alternative method for classifying the architecture of not only angiospermous but all megaphyllous leaves. Hickey (1979) stated that this scheme would not be useful to palaeobotanists studying angiosperm leaves because important characters unique to angiosperms are disregarded.

3.2.2.1 Spicer's terminology

There have been more recent attempts at defining terminology for angiosperm leaf architecture prompted by the sometimes difficult, but necessary, identification of vein orders and consequential problems of defining leaf venation type in Hickey's scheme. Spicer (1986c) erected new terminology using 'pectinal' veins to remove the problem of distinguishing between intergrading primary and secondary vein orders and pinnate and palmate venation in mid-Cretaceous leaves, which show continuous variation in venation patterns. Pectinal veins are identified as the veins diverging from the midvein having the greatest number of abmedial branches (outer secondary veins) and are described in terms of the proportion of the lamina area that they or their branches serve. This means that these terms cannot be easily applied to these Antarctic Cretaceous leaves which are fragmentary and often have the basal part of the leaf missing. For these fragmentary leaves it is more useful to define vein orders using relative vein widths, supplemented by considerations of geometry. For example, Morphotype 31 (Figure 5.20f,g, Chapter 5) cannot be described in terms of pectinal veins because the basal part of the leaf is incomplete, but can be defined as palmate based on an assessment of relative vein thickness.

3.2.2.2 Pole's terminology

Pole (1991) presented a set of modifications to Hickey's classification for describing leaf architecture based on a hypothetical sequence of ontogenetic or phylogenetic lamina development, with emphasis placed on patterns formed by groups of venation elements rather than vein size. To avoid the problem of distinguishing between lateral primaries and basal secondaries, this scheme rules that there is only one primary vein in a leaf, the midvein, and the palmate conditions of Hickey's scheme, actinodromous and acrodromous venation, are expressed as development of craspedodromous and camptodromous venation, respectively. However, the identification of actinodromous or acrodromous development is highly subjective because these are recognised only by strong development of basal lateral veins. Relative vein thickness still plays an important role throughout this terminology and there are the same ambiguities of intergrading categories. Pole's scheme was not used because this terminology has not been widely adopted and it offered no particular advantages in this study of Antarctic Cretaceous leaves.

Both Spicer's (1986c) and Pole's (1991) character definitions are restricted to venation patterns and must be used in tandem with Hickey's scheme for describing other leaf features, such as shape. The principal reason for not using these schemes was because of their incompatibility with much of the literature on fossil and living angiosperm floras, but a comprehension of Spicer's and Pole's terminology was necessary to allow comparison with the work of these authors on Cretaceous angiosperm leaves. The same applies to the classification proposed by Klucking (1995), based on phases of ontogenetic development in leaf venation. Klucking has, however, also provided much useful information using this scheme on the leaf venation patterns of many living angiosperm families (1986-1997).

3.2.3 The advantages of adopting Hickey's terminology for this study

I chose the classification outlined by Hickey (1973, 1979) in this study of Cretaceous Antarctic angiosperm leaves for three reasons. Firstly, it provides a comprehensive detailed terminology that can be used to precisely describe the features of leaf outline and venation that are well preserved in these fossils. The approach to partitioning these angiosperm leaf fossils ultimately used in this study (Chapter 4) does not rely solely on the first and second order venation pattern and it is the whole suite of characters in Hickey's scheme that are very useful. Secondly, the terms defined have been proved valuable because they were shown to be important for description or systematics in Hickey's study of herbarium specimens from approximately 1850 genera in 192 families. A third reason for using this scheme is to facilitate comparison with other fossil and living floras, since many studies are based on standardised observations using Hickey's classification. Examples include Zastawniak's (1994) study of Cretaceous leaves from the Antarctic Peninsula and Hill's (1983, 1986) studies of Tertiary leaves from Australia.

3.3 Elements of Hickey's classification for angiosperm leaves useful in this study

The main features of Hickey's scheme are outlined as an illustrated glossary in Appendix 1. Although there were some difficulties experienced using Hickey's (1973, 1979) classification, the majority of its elements have been useful in this study of Cretaceous Antarctic angiosperm leaves. Below are some comments on their value in this study of Antarctic angiosperm leaves.

- Leaf orientation (Appendix 1, Figure A-1) – standard terms for defining axes of orientation and curvature of leaf elements useful in describing these Cretaceous leaves.

- Leaf organisation (Appendix 1, Figure A-2) – not useful because there are no compound leaves found intact within these Cretaceous Antarctic floras. It is not possible to determine whether a fossil leaf is truly simple or is a fragment of a compound leaf.

Leaf shape:
- Lamina symmetry (Appendix 1, Figure A-3) – descriptive terms easily used when the midvein and margin of a fossil leaf is clearly preserved. For fragmentary specimens, these terms are much more difficult to apply. In the many cases where much of one side of a leaf is missing, it is clearly not possible to estimate whether a leaf is symmetrical or not. For leaves with clear margins preserved on both sides of the lamina, the apex and/or base are often missing. Amongst these specimens, the recognition of asymmetry can be taken to indicate that the leaf is asymmetrical, however, the recognition of symmetry in the part of the leaf preserved cannot be taken to indicate that the whole lamina is symmetrical. For this reason it is to be expected that the results show a bias towards asymmetrical leaves. ·

- Form (Appendix 1, Figure A-4) – length, width and position of maximum width was measured for all the leaf specimens. The forms of almost whole leaves were easily defined. For incomplete leaves, although in some cases the maximum width of the leaf was clearly preserved, the total length was not obtainable. Levels of uncertainty in leaf form determination have been recorded in the descriptions. In some cases it was possible to confidently estimate lamina form from the curvature of the margins present in fragmentary specimens. Length/width ratios were calculated for the fossil leaves and the terms defined in Table A-1 (Appendix 1) were used to name leaf form. There were some problems encountered when using this table since there are some gaps, e.g. for an oblong leaf with a length/width ratio of 1.4:1 it was not clear how this should be named, so in these cases, I have used the term nearest to the measured ratio.

- Apex and Base (Appendix 1, Figure A-5 and Figure A-6) – bases have been preserved in 40-50% of the Antarctic specimens and apices are present in approximately 25% of the leaves, so these terms were useful. However, Hickey's definition of the apex and base caused difficulties when measuring angles. Even though the apex or base may be present, since many of the leaves are incomplete it is not clear how much of the leaf is delimited by

25% of the margin. In these cases, the reconstructed leaf outline was used to assess these portions and measurements gave estimates of the apical and basal angles. The apical and basal styles defined by Hickey can, however, be much more confidently estimated for fragmentary specimens and are therefore much more useful characters than quantitative measurements.

Palaeoclimate interpretation models based on leaf physiognomy use slightly different terminology for the shape of the leaf apex and base and these are taken into account in the palaeoclimate studies presented in Chapter 6.

- <u>Form of leaf margin</u> (Appendix 1, Figure A-7, Figure A-8 and Figure A-9) – marginal features are important in Hickey's classification and are commonly used by palaeobotanists. These terms have been very useful in this study because these characters are of value in identifying even fragmentary leaves (e.g. Morphotype 39, Figure 5.23b,c, see Chapter 5). Features of marginal teeth have been found to be especially useful in dicotyledonous angiosperm leaf systematics (Hickey and Wolfe 1975). Teeth can be described using the same terms used to describe leaf apices, e.g. angle and style of tooth apex, and serration type is categorised by the shape of the basal side of the tooth versus the shape of the apical side. There is a bias with these fragmentary specimens when only a small proportion of the margin is preserved. It is far easier to confidently describe a leaf as toothed than entire. Lobes are also difficult to recognise in such fragmentary specimens. A toothed margin may also have been mistaken for an erose or crenate margin because of poor preservation of the specimen.

Leaf margin analysis is important for fossil plants for classification and palaeoclimatic analysis. Palaeoclimate studies implement different methods to differentiate between entire and non-entire margins (see Chapter 6). The recognition of lobes is also different. (In Hickey's scheme a lobe is distinguished from a tooth by the distance the margin is indented towards the long axis of the leaf. In order to distinguish between lobes and teeth Wolfe (1993) draws lines joining the sinuses along each side of the lamina. If these lines are parallel, the leaf is defined as lobed, if not, the projections are defined as teeth.) These different approaches are taken into account in the palaeoclimatic interpretations in Chapter 6.

- <u>Leaf texture</u> – there are definitions that can be used for modern leaves and rare mummified leaves, but it is not possible to apply them to these Antarctic angiosperm leaf impressions. Since these Cretaceous fossils are preserved as impressions with a thin carbonaceous film or calcareous mineralisation there is no indication of the original thickness of the leaf. Comparisons can be drawn between the leaf remains within a flora, such as the Hidden Lake Formation flora, but this is unreliable. It is sometimes possible to detect thick leaves within this type of fossil flora by the appearance of wrinkling in the leaf (Cantrill and Nichols 1996). Although this was observed in some of the bennettitalean foliage within these floras, it was not recognised in any of the dicotyledonous angiosperm leaves.

- <u>Gland position</u> (Appendix 1, Figure A-10) – there are several possible positions for glands on leaves. In fossils these sometimes appear as a dark stain produced by the gland contents (Cantrill and Nichols 1996). These Antarctic leaves were examined for the possible presence of glands and concentrations of dark material indicate that some teeth may show glands, e.g. D8754.8.9a (Morphotype 25, Figure 5.18, Plate 2.1C). One possible representative of gland preservation on the laminae of these Late Cretaceous leaf specimens is D8605.21Aa&Ba (Morphotype 24, Figure 5.17b,c).

- <u>Petiole</u> (Appendix 1, Section A6) – petioles are present in 10-15% of the Antarctic leaves, occurring in 20-30% of the leaves in which bases are preserved. Although fossil preservation prevents confident determination of petiole type, normal and possibly winged petioles were observed. It was not possible to confidently recognise inflated or thickened petioles in these impression fossils. For isolated leaf fossils it is not possible to distinguish between a leaf where the petiole is truly absent, with the lamina attached directly to the stem, and a leaf where the petiole has been lost in the preservation process. In this study, if a leaf base is clearly preserved without a petiole, the petiole is defined as absent.

- <u>Types of venation</u> (Appendix 1, Section A7, Figure A-11) – the configuration of the primary and secondary veins determines the major vein classes. It was possible to follow Hickey's classification, but it was very difficult to confidently determine the venation pattern of fragmentary specimens. The venation pattern formed by the primary and secondary veins can only really be confidently assessed for almost complete leaves. For most specimens, at least the base of the leaf is needed to establish the number of primary veins, which is a starting point for this classification. For example, in D8754.8.6b&65a, (Morphotype 25, Figure 5.17e,f), the venation is described as pinnate simple craspedodromous, but the base of the leaf is not preserved, so the possibility that the leaf is actinodromous cannot be eliminated. In less well preserved leaves it is also very difficult to distinguish between pinnate camptodromous brochidodromous and pinnate camptodromous eucamptodromous venation (e.g. D8754.8.40a, Appendix Volume 2 p27, 101).

It is fundamental in Hickey's classification that vein orders are recognised, but one of the most difficult aspects of this scheme is assigning vein orders. In some cases the decision as to whether a vein is primary or secondary is rather subjective, especially when the preservation of the leaf impression fossils is less than ideal. Leaf drawings alone are insufficient for vein order to be assigned and precise comparative assessment of vein thickness must be made from the original specimens and photographs. For example, in D8754.8.1a (Morphotype 2, Plate 3.4A, Figure 5.2d) it is difficult to distinguish basal imperfect marginal actinodromous venation from pinnate mixed craspedodromous venation. The lowest pair of vein branches does appear slightly thicker than those above, so it is determined that the venation is actinodromous.

In specimens where the midvein is not completely preserved and its width cannot be compared to that of its branches, then the order of the branch is estimated by comparison with the width of branches from the midvein in other specimens. For example, specimen D8754.8.4d (Morphotype 4, Appendix Volume 2 p4, 66) is a fragment from the base of a leaf, the midvein is only partially preserved and there is one prominent branch from the midvein close to the base of the leaf. It is unclear, therefore, whether this branch is a primary or secondary vein. This fragmentary specimen is very close in size and shape to the basal part of D8754.8.60a (Morphotype 8, Figure 5.8b, Plate 3.11C), and both specimens have a toothed margin. The lowest branch from the midvein in D8754.8.60a is clearly a secondary vein. It is also thicker than the vein branch in question in D8754.8.4d. For this reason, it is estimated that the branch from the midvein in D8754.8.4d is a secondary vein. However, these two leaf specimens are from different taxa and the widths of primary, secondary and tertiary veins have been shown to vary between taxa (Hickey 1973), so this is not a completely confident estimation.

Orders of venation – there are sets of definitions for each vein order, set out in Appendix 1, Figures A-12 to A-23.

- Primary veins (Appendix 1, Section A8.1, Figure A-12) – there are terms applicable to the thickness and course of the primary veins. Where leaf length is incomplete in these Cretaceous specimens, the size of the primary is measured at the estimated leaf midpoint. If the primary vein is incomplete at the approximate midpoint, then measurements are made at a point slightly closer to the apex or base where the primary vein is clear. In the cases where the margin is incomplete at the approximate midpoint, then if possible, leaf width is estimated from the curvature of margin present. If this is not possible then measurements of vein and leaf width are made where margin is preserved on at least one side of the leaf. There is a bias against recognition of straight primary veins. It is far easier to confidently recognise a curved primary vein from a fragmentary specimen than it is to recognise a straight vein.

- Secondary veins (Appendix 1, Section A8.2, Figures A-13 to A-17) – there are terms applicable to the angle of divergence of the secondary veins from the midvein and the secondary vein course. At first, the angles of divergence of all preserved secondary and tertiary veins in these leaf specimens were measured and the average was used in the classification of leaves. However, it became apparent that comparisons on this basis were not possible. In many dicotyledonous angiosperm leaves there is a variation in divergence angle of secondary veins along the length of the lamina. However, in a significant proportion of these fragmentary fossil leaves, the apex or base or both are missing. For this reason, the measurements used were taken from the middle parts of the leaf and those measurements made from the apical or basal parts of the leaf were excluded in the average secondary vein measurement. A separate measurement of basal secondary vein angle was made because the basal pair of secondary veins in angiosperm leaves frequently arise from the midvein at a markedly different angle to the secondaries above (Hill 1980a). Including

measurements of the basal vein in the average of all veins would therefore clearly produce problems, since in at least 50% of the specimens the base is not clearly preserved. The terms describing secondary vein course have generally been useful and easily applied in this study of Late Cretaceous fossil leaves.

- Tertiary veins (Appendix 1, Section A8.3, Table A-2, Figures A-18 to A-19) – there are terms applicable to the angle of origin of tertiary veins on the admedial and exmedial sides of the secondary veins and on the midvein, along with terms applicable to tertiary vein patterns. Tertiary veins were a useful feature in describing these specimens because they are clearly preserved in many of these Cretaceous leaves. To reduce the possible effects of occasionally incorporating angle measurements from preservational features, which had been mistakenly identified as veins, a series of measurements were made and the average taken. The tertiary vein angles used to calculate averages were also restricted to those measured in the middle part of the leaves. In some leaves the tertiary vein angle varies either apically or exmedially, so this was considered necessary when dealing with a flora containing fragmentary specimens. Although tertiary veins are clearly preserved, the tertiary venation pattern frequently appears rather poorly developed in comparison to modern angiosperm leaf architecture. The tertiary venation pattern was examined for all leaf specimens, but was not used to partition these Late Cretaceous leaves into taxa.

- Higher order venation patterns and tooth architecture (Appendix 1, Sections A8.4 and A9, Figures A-20 to A-25) – there are terms applicable to the patterns formed by quaternary and quinternary veins, marginal ultimate venation, areolation and tooth architecture. These features could be recognised in many of these Cretaceous Antarctic leaves. The higher order venation features and tooth architecture could not be described for every specimen. The description of these features is based on the best preserved leaves within the floras. Since features of the tertiary and higher order venation patterns and tooth architecture were not actually used in the partitioning of angiospermous leaf taxa, the comparison of these features amongst specimens of a morphotype were a reassuring confirmation of the method used to differentiate leaf taxa.

Leaf rank:

Leaf rank categories defined by Hickey (1977) are also used in the description of these leaves and these are illustrated in Appendix 1B. These terms are commonly used by palaeobotanists (e.g. Taylor and Hickey 1990) and have been used in assessments of primitive versus advanced features of dicotyledonous angiosperm leaves (Hickey and Wolfe 1975, Wolfe et al. 1975). These terms reflect the progressive increases in venation organisation believed to have occurred in all angiosperm groups, with the primitive condition remaining only within some Magnoliales, e.g. Winteraceae. The leaves of some Nothofagus species are an example of high rank (Doyle and Hickey 1976, Hickey 1977).

3.4 Description of the Antarctic angiosperm specimens

All the Cretaceous Antarctic angiosperm leaves were described using the terms from Hickey's (1973, 1979) classification. A total of 94 leaves were described for the Hidden Lake Formation flora and 99 for the Santa Marta Formation flora. One example is given on the following page but for brevity the remainder are presented in Appendix Volume 2. A summary table of the main features of all the leaves studied is presented in Table 3.1.

For each leaf there is a description and a line drawing obtained using a stereo research microscope and a drawing tube. With repeated observations with lighting at various angles and evidence from photographs, it was generally possible to distinguish between veins and preservational features and the different orders were marked on the drawings in different colours (see Appendix Volume 2). The collection of this data was very time consuming, but it is believed that such a rigorous approach provides more accurate and useful information and allows clearer comparison with other angiosperm leaves. The more information available from a detailed study of a fossil leaf form, the better it can be compared to living taxa and other fossil leaf forms.

Photographs of representative leaf fossils from these Late Cretaceous floras are presented in the following pages. Photographs of most of the morphotypes are included, but some are omitted because, as discussed in Chapter 2, the nature of preservation and the uneven surfaces of the fossils meant that it was difficult to obtain photographs clearly showing characteristic architectural features for all of the leaves. The photographs serve to illustrate the style and level of preservation of leaf architecture in the Hidden Lake Formation and Santa Marta Formation floras and are intended to create a clear impression of the leaf material available for study.
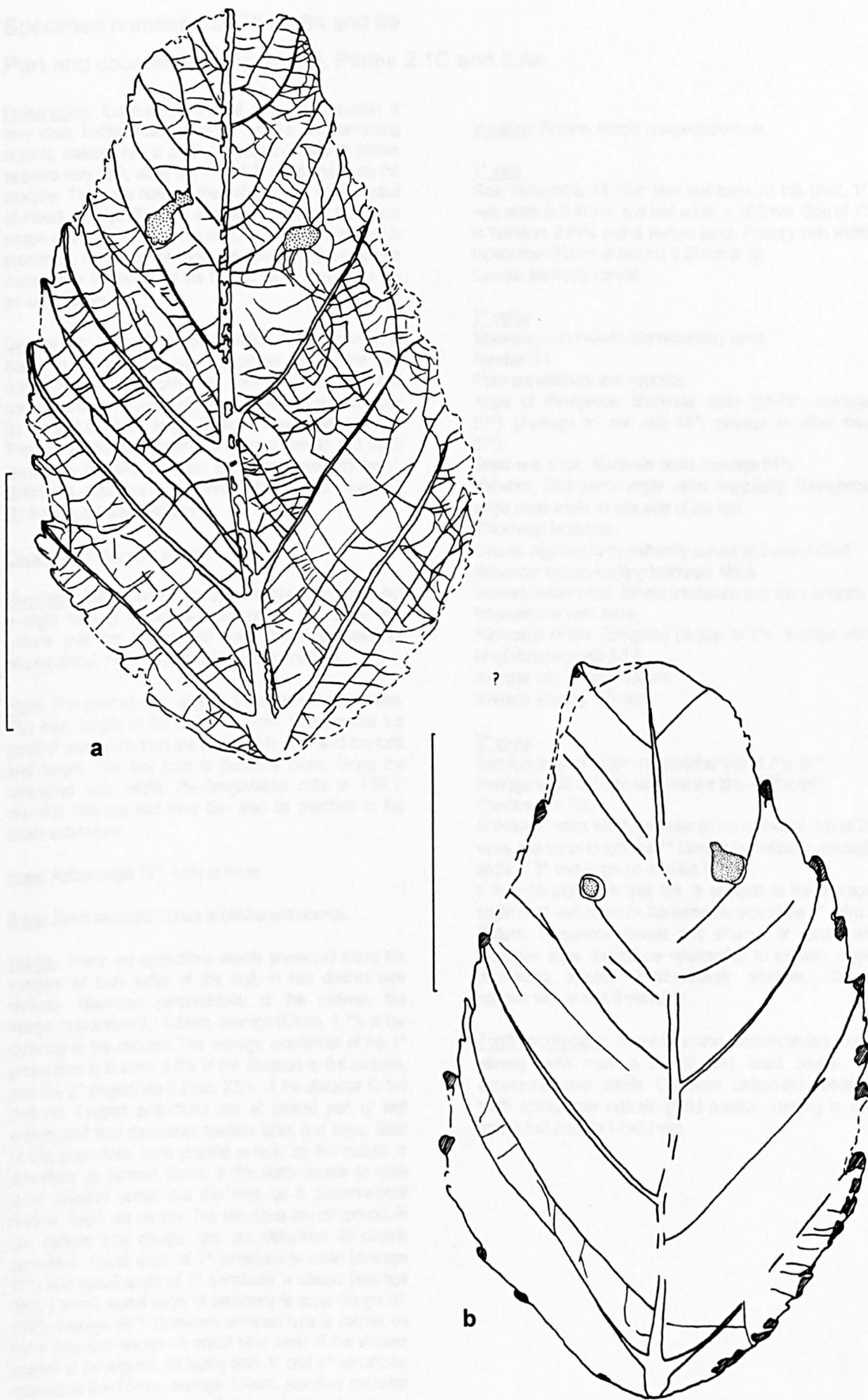
Figure 3.3 Morphotype 25. (a) D8754.8.8a. (b) D8754.8.9a.
Scale bar is 10mm.

Specimen numbers: D8754.8.8a and 9a

Part and counterpart. Figure 3.3. Plates 2.1C and 3.6A.

Preservation: Excellent (8a), good (9a). The venation is very clear, better preserved in 8a than 9a. The remaining organic material has a patchy appearance and in places appears very dark, along the 1° and 2° veins and along the margins. There are holes in the leaf that may be the result of insect damage. The leaf is almost whole and the whole shape can be observed. The majority of the leaf margin is preserved, clearer in 9a. Both the apex and base appear complete in 9a, but in 8a the tip and basal margin are not as well preserved.

Dimensions: Although the preservation of the venation is better in 8a and the apex is clearer in 9a, the leaf completeness is roughly the same in the part and counterpart, so the measurements given here are averages for 8a and 9a. Max. length 29.4mm. Max. width 17.7mm. The leaf is almost complete so the max. length and width appear to be fairly accurate estimates. Area 355.4mm². Estimated max. area 355.8mm². Max. length along 1° 29.4mm. 'Leaf area' 346.2mm².

Organisation: Appears simple.

Symmetry: Whole lamina appears roughly symmetrical but a slight 'bulging' in the lower part of one side of the leaf means that the lamina and base are categorised as asymmetrical. Apex appears slightly asymmetrical.

Form: The point of max. width is 11mm from the leaf base. The max. length of the leaf is 29.4mm, meaning that the point of max. width from the leaf base is at 37% of the total leaf length. The leaf form is therefore ovate. Using the estimated max. width, the length/width ratio is 1.66:1, showing that the leaf form can also be ascribed to the ovate subdivision.

Apex: Apical angle 75°. Apex is acute.

Base: Basal angle 98°. Base is obtuse and normal.

Margin: There are projections clearly preserved along the margins of both sides of the leaf, in two distinct size classes. Measured perpendicular to the midvein, the margin is indented 0.1-0.8mm, average 0.3mm, 4.7% of the distance to the midvein. The average indentation of the 1° projections is 0.4mm, 5.8% of the distance to the midvein, and the 2° projections 0.2mm, 2.9% of the distance to the midvein. Largest projections are at central part of leaf margin and size decreases towards apex and base. Most of the projections have pointed apices, so the margin is described as toothed. Some of the teeth appear to have quite rounded apices but this may be a preservational feature. Teeth are serrate. The serrations are compound, in two definite size groups, and are described as double serrations. Apical angle of 1° serrations is acute (average 77°) and apical angle of 2° serrations is obtuse (average 95°). Overall, apical angle of serrations is acute (range 30-149°, average 84°). Dominant serration type is convex on basal side and convex on apical side. Most of the sinuses appear to be angular. Including both 1° and 2° serrations, spacing is 0.4-3.6mm, average 1.4mm, standard deviation 0.7mm, and spacing is described as irregular. Spacing of 1° projections only is 0.7-4.5mm, average 2.3mm, standard deviation 0.9mm, and spacing is still described as irregular.

Petiole: Absent or not preserved.

Venation: Pinnate, simple craspedodromous.

1° vein:
Size: Midpoint is 14.7mm from leaf base. At this point, 1° vein width is 0.47mm and leaf width is 16.3mm. Size of 1° is therefore 2.89% and is termed stout. Primary vein width tapers from 0.9mm at base to 0.25mm at tip.
Course: Markedly curved.

2° veins:
Measurements include intersecondary veins.
Number: 24.
Pairs are alternate and opposite.
Angle of divergence: Moderate acute (24-73°, average 53°). (Average on one side 48°, average on other side 57°).
Basal vein angle: Moderate acute (average 51°).
Variation: Divergence angle varies irregularly. Divergence angle more acute on one side of the leaf.
Thickness: Moderate.
Course: Appears to be uniformly curved and unbranched.
Behaviour of loop-forming branches: None.
Intersecondary veins: Simple intersecondary veins present.
Intramarginal vein: None.
Intercostal shape: Elongated parallel to 2°s, average vein length/spacing ratio 5.5:1.
Average vein length: 12.2mm.
Average spacing: 3.5mm.

3° veins:
Average angle of origin on admedial side of 2°s: 94°.
Average angle of origin on exmedial side of 2°s: 98°.
Combination: RR.
In those 3° veins which originate on the admedial side of 2° veins and curve to join the 1° forming the midvein, average angle of 3° vein origin on midvein is 119°.
It may be significant that this is unequal to the average angle of 3° vein origin on the exmedial side of the 2° veins.
Pattern: Percurrent. Simple and sinuous or retroflexed. Tertiaries show an oblique relationship to midvein, angle decreasing apically. Predominantly alternate. Closely spaced, with at leas 6 veins/cm.

Tooth architecture: Secondary and intersecondary veins serving teeth have a central and direct course. No accessory veins visible. Darkened carbon-rich areas in tooth apices may indicate gland position, ranging in size from 0.5x0.2mm to 1.0x0.7mm.

Plate 3.3

3A. D8754.8.35a. Hidden Lake Formation flora. Morphotype 1.
     Scale bar 5mm.

3B. D8754.8.67a. Hidden Lake Formation flora. Morphotype 1.
     Scale bar 5mm.

3C. D8754.8.30a. Hidden Lake Formation flora. Morphotype 20.
     Scale bar 5mm.

3D. D8754.8.3a. Hidden Lake Formation flora. Morphotype 2.
     Scale bar 5mm.
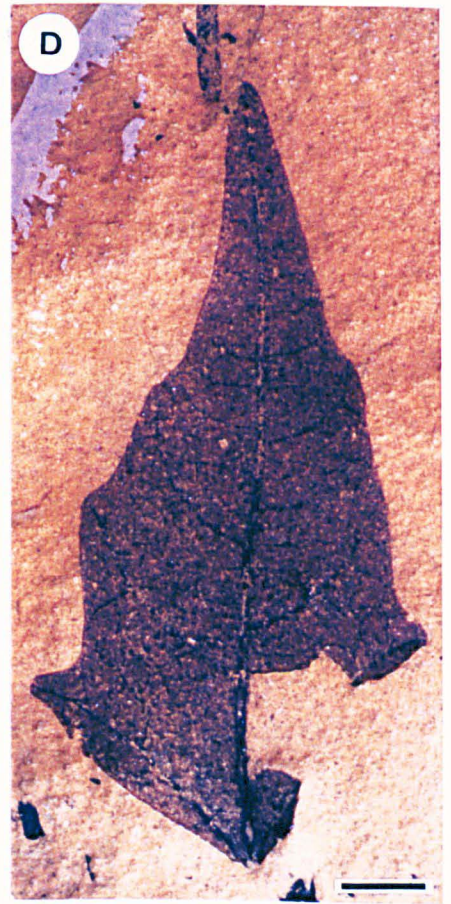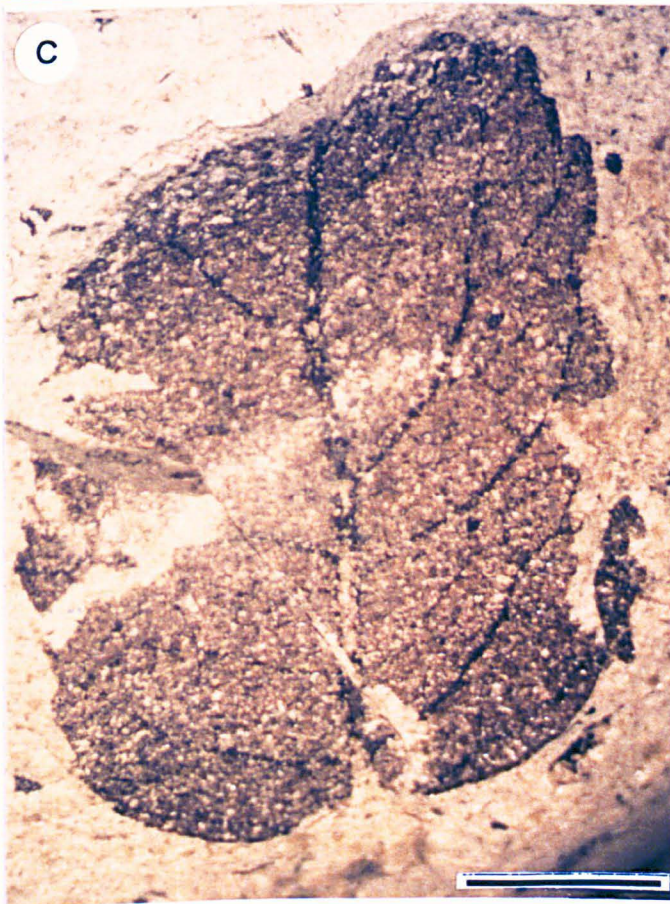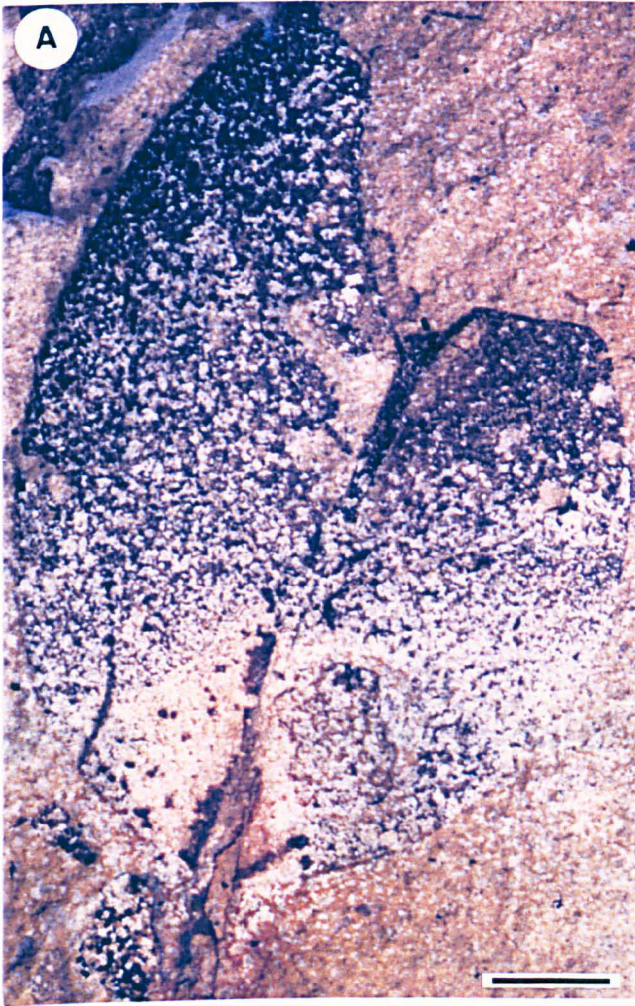
Plate 3.4

4A.   D8754.8.1a. Hidden Lake Formation flora. Morphotype 2.
         Scale bar 5mm.

4B.   D8754.8.45a. Hidden Lake Formation flora. Morphotype 3.
         Scale bar 5mm.

4C.   D8754.8.6b. Hidden Lake Formation flora. Morphotype 25.
         Scale bar 5mm.

4D.   D8754.8.43a. Hidden Lake Formation flora. Morphotype 36.
         Scale bar 5mm.
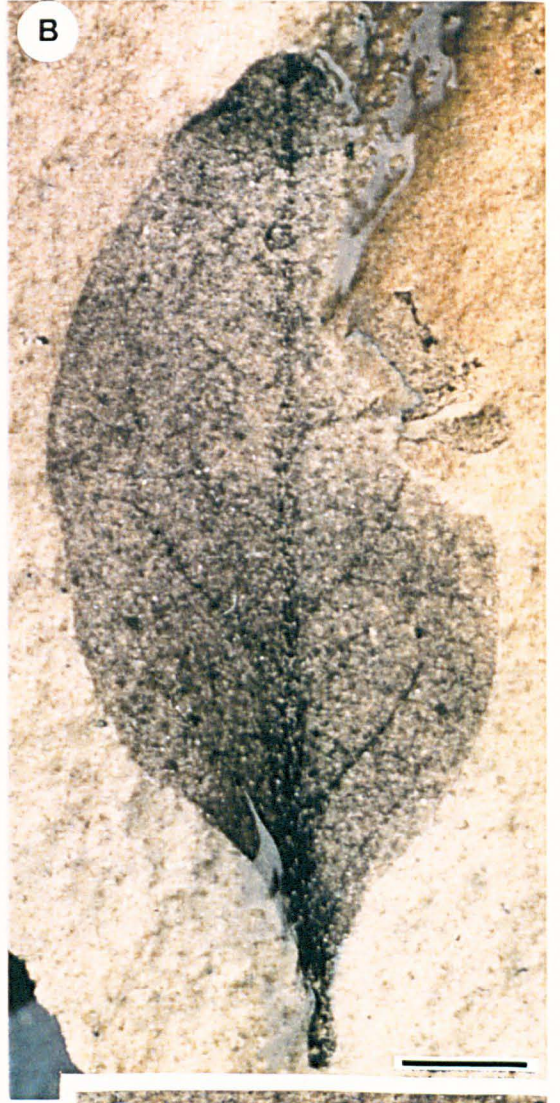
Plate 3.5

5A.   D8606.7Aa. Santa Marta Formation flora. Morphotype 4.
        Scale bar 5mm.

5B.   D8754.8.4a. Hidden Lake Formation flora. Morphotype 17.
        Scale bar 5mm.

5C.   D8604.38Aa. Santa Marta Formation flora. Morphotype 29.
        Scale bar 5mm.

5D.   D8604.54a. Santa Marta Formation flora. Morphotype 13.
        Scale bar 5mm.

Plate 3.6

6A.   D8754.8.8a. Hidden Lake Formation flora. Morphotype 25. Scale bar 5mm.

6B.   D8754.8.54a. Hidden Lake Formation flora. Morphotype 11. Scale bar 5mm.

6C.   D8610.1Aa. Santa Marta Formation flora. Morphotype 5B. Scale bar 5mm.

6D.   D8754.8.41a. Hidden Lake Formation flora. Morphotype 5B. Scale bar 5mm.

Plate 3.7

7A.   D8616.74a. Santa Marta Formation flora. Morphotype 12. Scale bar 5mm.

7B.   D8754.8.34a. Hidden Lake Formation flora. Morphotype 7. Scale bar 5mm.

7C.   D8604.39a. Santa Marta Formation flora. Morphotype 24. Scale bar 5mm.

7D.   D8754.8.28a. Hidden Lake Formation flora. Morphotype 15. Scale bar 5mm.

7E.   D8754.8.16b. Hidden Lake Formation flora. Morphotype 9. Scale bar 2.5mm.
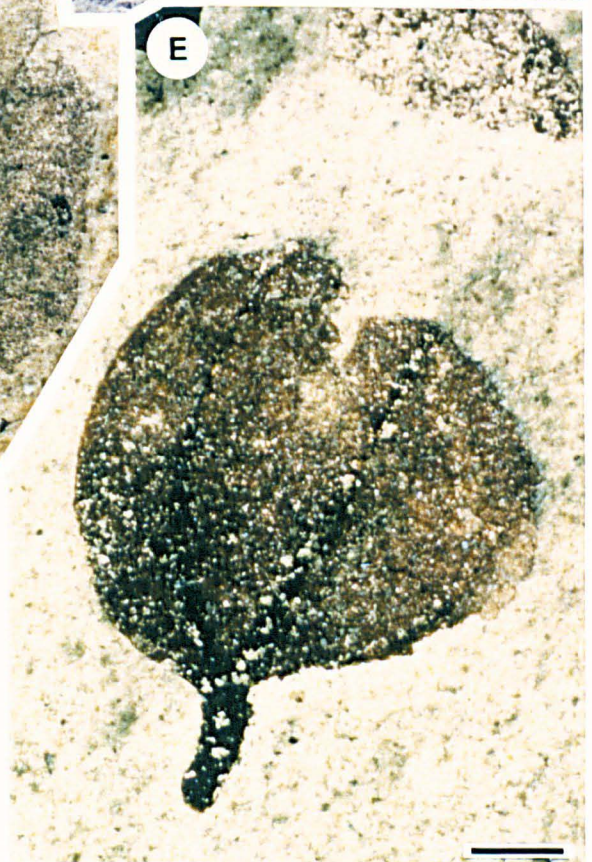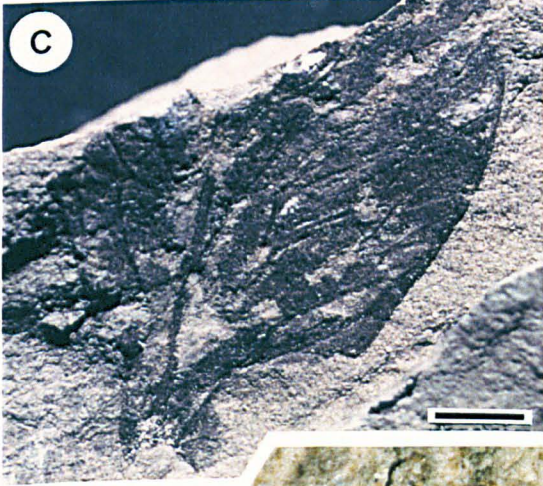
Plate 3.8

8A.   D8621.27a. Santa Marta Formation flora. Morphotype 7.
        Scale bar 5mm.

8B.   D8754.8.42a. Hidden Lake Formation flora. Morphotype 10.
        Scale bar 5mm.

8C.   D8619.6a. Santa Marta Formation flora. Morphotype 12.
        Scale bar 5mm.

8D.   D8616.128a. Santa Marta Formation flora. Morphotype 7.
        Scale bar 5mm.

Plate 3.9

9A.   D8754.8.48a. Hidden Lake Formation flora. Morphotype 28.
        Scale bar 5mm. .

9B.   D8754.8.31a. Hidden Lake Formation flora. Morphotype 20.
        Scale bar 5mm.

9C.   D8604.37A/Ca. Santa Marta Formation flora. Morphotype 13.
        Scale bar 5mm.

9D.   D8754.8.57a. Hidden Lake Formation flora. Morphotype 11.
        Scale bar 5mm.
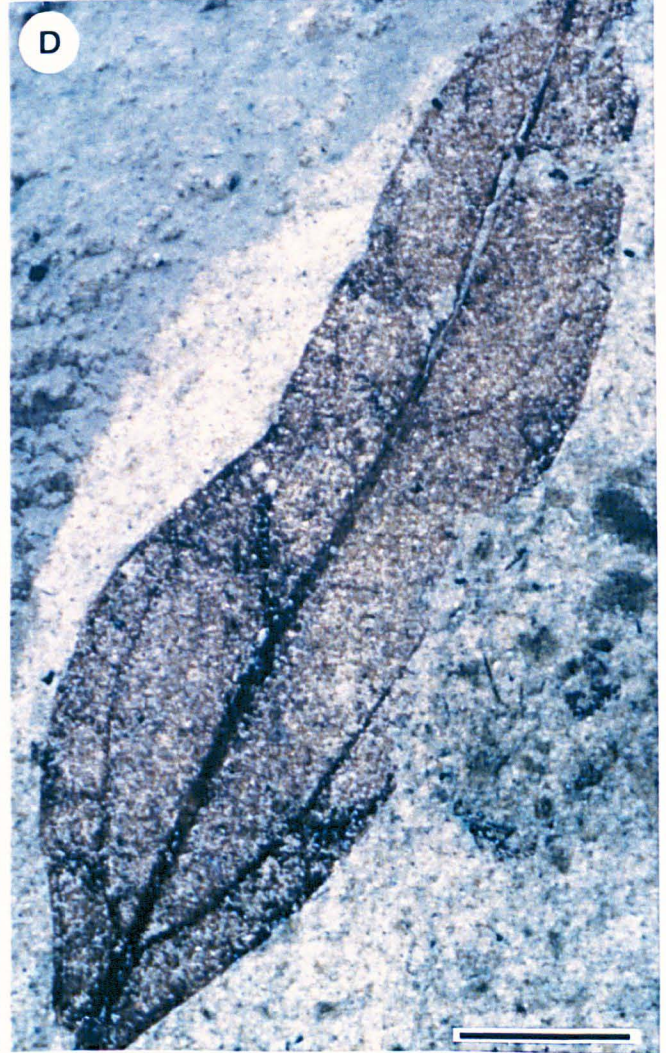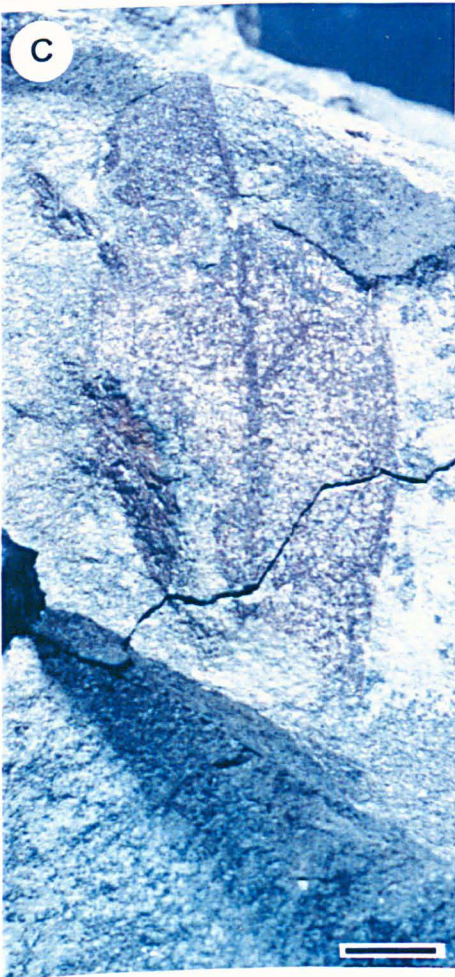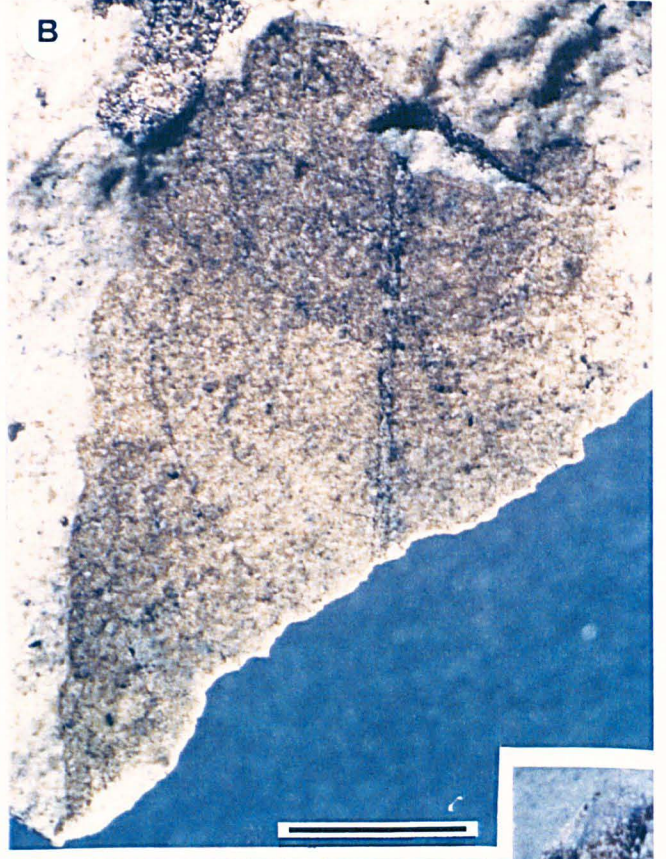
Plate 3.10

10A. D8754.8.34b. Hidden Lake Formation flora. Morphotype 39.
      Scale bar 2.5mm.

10B. D8605.2a. Santa Marta Formation flora. Morphotype 18.
      Scale bar 5mm.

10C. D8609.147a. Santa Marta Formation flora. Morphotype 28.
      Scale bar 2.5mm.

10D. D8605.15a. Santa Marta Formation flora. Morphotype 3.
      Scale bar 5mm.

Plate 3.11

11A.   D8754.8.62a. Hidden Lake Formation flora. Morphotype 32.
Scale bar 5mm.

11B.   D8754.8.4c. Hidden Lake Formation flora. Morphotype 14.
Scale bar 5mm.

11C.   D8754.8.60a. Hidden Lake Formation flora. Morphotype 8.
Scale bar 10mm.

11D.   D8754.8.63a. Hidden Lake Formation flora. Morphotype 35.
Scale bar 10mm.

11E.   D8754.8.39a. Hidden Lake Formation flora. Morphotype 34.
Scale bar 2.5mm.
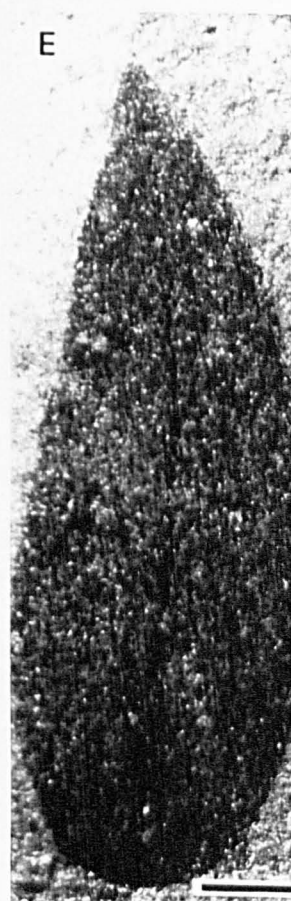
Table 3.1 Summary of the architectural features present in these Antarctic Cretaceous fossil leaves.

HLF = Hidden Lake Formation flora, SMF = Santa Marta Formation flora. Data indicate numbers of specimens possessing each feature.

Character	State	HLF	SMF
Whole lamina symmetry	Symmetrical	1	2
	Asymmetrical	19	18
	Unclear	74	79
Basal symmetry	Symmetrical	5	10
	Asymmetrical	11	8
	Unclear	78	81
Apical symmetry	Symmetrical	4	9
	Asymmetrical	2	7
	Unclear	88	83
Lamina form	Oblong	3	8
	Elliptic	2	3
	Ovate	12	9
	Obovate	1	0
	Unclear	76	79
Apex form	Acute	2	7
	Acuminate	2	0
	Attenuate	3	12
	Obtuse	0	2
	Emarginate	0	1
	Unclear	88	77
Base form	Acute normal	0	10
	Acute cuneate	9	8
	Acute decurrent	12	7
	Obtuse normal	8	4
	Obtuse cuneate	3	3
	Rounded	2	1
	Cordate	3	1
	Lobate	0	1
	Hastate	0	1
	Unclear	57	63
Margins	Entire	20	40
	Lobed	2	5
	Toothed	13	20
	Crenate	11	8
	Erose	2	3
	Unclear	46	23
Petiole	Present	14	10
	Absent	23	28
	Unclear	57	61
Venation pattern	Pinn. simp. crasp.	6	12
	Pinn. semicrasp.	2	8
	Pinn. mixed crasp.	1	0
	Pinn. camp. broch.	17	26
	Pinn. camp. euc.	4	3
	Pinn. camp. retic.	0	3
	Acrodromous	6	4
	Actinodromous	6	4
	Palinactinodromous	2	2
	Unclear	50	37
Primary vein size	Massive	12	19
	Stout	29	42
	Moderate	12	7
	Weak	1	6
	Unclear	40	25

Character	State	HLF	SMF
Primary vein course	Straight	35	41
	Curved	27	21
	Sinuous	0	0
	Zigzag	0	0
	Unclear	32	37
Secondary vein divergence angle	Narrow acute	9	24
	Moderate acute	31	32
	Wide acute	19	17
	Right-angled	4	4
	Obtuse	0	0
	Unclear	31	22
Basal secondary angle	Narrow acute	17	19
	Moderate acute	13	9
	Wide acute	7	4
	Right-angled	0	2
	Obtuse	0	0
	Unclear	57	65
Variation in secondary divergence	Nearly uniform	2	14
	Upper more obtuse	3	8
	Upper more acute	2	2
	Lowest pair more acute	11	6
	Lr. and up. more obtuse	0	0
	Irregular	18	32
	Unclear	58	37
Symmetry of secondary divergence	Symmetrical	19	37
	Asymmetrical	30	24
	Unclear	45	38
Secondary vein course	Straight	0	5
	Recurved	8	14
	Curved	51	60
	Sinuous	4	7
	Zigzag	0	0
	Unclear	31	13
Secondary vein branching	Unbranched	26	26
	Branched	32	54
	Unclear	36	19
Outer secondary veins	Absent	88	77
	Present	6	9
	Unclear	0	13
Intersecondary veins	Absent	32	41
	Present	17	39
	Unclear	45	19
Intramarginal vein	Absent	55	69
	Present	1	3
	Unclear	38	27
Admedial tertiary angle	Acute	21	20
	Right-angled	44	63
	Obtuse	9	9
	Unclear	20	7
Exmedial tertiary angle	Acute	45	47
	Right-angled	25	42
	Obtuse	5	4
	Unclear	19	6
Midvein tertiary angle	Acute	21	28
	Right-angled	24	32
	Obtuse	4	11
	Unclear	45	28

Table 3.1 is a summary of the features present in the Antarctic Cretaceous fossil leaves. This table clearly illustrates the preservational difficulties encountered in the study of these Late Cretaceous fragmentary transported assemblages. The proportion of leaves with characters missing is discussed in Chapter 2 and Chapter 4.

Table 3.1 highlights the similarity in the distribution of leaf architectural characteristics between the two floras. For each character, the dominant state is generally the same for both the Hidden Lake Formation and the Santa Marta Formation floras. The clearly dominant characteristics of these Late Cretaceous leaves are an asymmetrical lamina, an entire margin, pinnate camptodromous brochidodromous venation, a stout straight midvein, narrow acute divergence of the basal secondary veins, curved secondary veins, and right angled origin of tertiary veins on the admedial side of the secondary veins. Within both floras, the possession of a petiole, outer secondary veins or an intramarginal vein are characters observed in only a relatively small percentage of the leaves.

The leaf apices are more frequently preserved in the Santa Marta Formation leaves than the Hidden Lake Formation leaves. The most frequently observed apex style in the Santa Marta Formation flora is attenuate. The two floras also show slightly different leaf base characteristics. The majority of leaves in both floras possess acute bases, but obtuse bases are more frequently observed in the Hidden Lake Formation leaves. One difference between the two floras is the basal symmetry, with the dominant state asymmetrical in the Hidden Lake Formation flora and symmetrical in the Santa Marta Formation flora. The dominant leaf shape is ovate in both floras, but an almost equal number of leaves have an oblong form in the Santa Marta Formation flora, which is a characteristic rarely observed in the Hidden Lake Formation flora. The Santa Marta Formation flora also shows a relatively high proportion of leaves with secondary veins diverging from the midvein at a narrow acute angle in comparison to the Hidden Lake Formation flora.

These Late Cretaceous leaf floras are fairly close together in geological time. The small differences outlined above may represent an evolutionary change in the flora, but it is expected that taphonomic controls (Chapter 7) and palaeoclimate (Chapter 6) will have had an effect on dominant leaf morphological characteristics.

3.5 Use of morphotypes in the identification of Late Cretaceous Antarctic angiosperm leaves

Dicotyledonous angiosperm leaves have been considered the most plastic and variable of all plant organs and leaf impressions the least diagnostic of all (Stebbins 1950 and Good 1966 in Dilcher 1974, Christophel 1976), so angiosperm systematics has generally been based on reproductive structures. There has been wide criticism of attempts by palaeobotanists to match Cretaceous and early Tertiary fossil angiosperm leaves to extant genera and families (see Dilcher 1974, Upchurch and Dilcher 1990). Hughes (1977) has asserted that it is only possible to recognise living angiosperm groups to the level of order in Late Cretaceous floras, but early

fossil leaf identifications were based on searches for the most similar modern family and genus. Early workers made general comparisons with the gross morphology of leaves of living plants and then assigned a modern name based on a best approximation, even when pertinent features were lacking. In this study of Cretaceous Antarctic angiosperms, the extensive works of Berry (1916-1945) on angiosperm leaves from the Cretaceous and Tertiary of South America were frequently consulted. Berry generally ascribed these fossils to modern genera, even when he doubted the relationships suggested. For example, Berry (1938) stated that the leaf fossils from the Tertiary of Argentina referred to *Myristica? fossilis*, were "equally like leaves in numerous other and unrelated genera". It is difficult to obtain useful information from these early reports of angiosperm leaves because the features of third and higher order venation are generally not described or illustrated, preventing comparison.

In the past, 'picture matching' has lead to misidentifications (Dilcher 1974). Without supporting evidence from detailed description and illustration, it is not possible to determine precisely which features were used in identification and the accuracy cannot be evaluated. For example, Orlando (1964) recorded angiosperm leaf species such as *Sterculia washburnii* from the Tertiary of King George Island, matching it to the species described from Patagonia by Berry (1938). There is no description or illustration of the King George Island fossils, prohibiting comparison, and the original description and illustration of the species by Berry (1938) also lacks detail.

Early records are therefore often considered unreliable and this must be taken into account. Darwin (1879) has frequently been quoted as calling the sudden appearance of 'advanced' extant angiosperm genera in the Cretaceous an "abominable mystery" (e.g. Axelrod 1952). Axelrod (1952) considered that the basic types must have already evolved by the time angiosperms appeared in the fossil record. The use of modern names, along with rare and now discredited pre-Cretaceous angiospermous fossils (Hughes 1977, 1994), provoked several theories to explain the apparent lack of ancestral angiosperm fossils, including the belief that early angiosperm evolution must have taken place in upland regions, away from sites favourable for preservation. However, from detailed studies of fine venation, it is now known that the earliest records of angiosperm leaves cannot be assigned to modern families (Wolfe *et al.* 1975, Doyle and Hickey 1976, Hickey and Doyle 1977). These authors demonstrated a sequence of progressive increases in regularity of form and venation in fossils from the Aptian to Cenomanian Potomac Group in North America.

In the search for the closest modern relative to a fossil leaf form, there is a clear bias towards forms with which the researcher is most familiar. This issue is illustrated in fossil floras from the Southern Hemisphere by the identification of poorly preserved leaves with pinnate craspedodromous venation as *Nothofagus*. This is a common component of Late Cretaceous and later floras in Antarctica but in many cases this assignment is unjustified because preservation is so poor that no diagnostic characters can be observed (Hill and Scriven 1995).

In order to work with fossil leaf forms without assigning them to a modern genus or species, many researchers use 'form genera'. A form genus is "a genus of fossil plants based on a detached organ which, because of the limited characters shown, cannot be assigned to a family, although it may be possible to assign it to a higher taxonomic level" (Jones and Rowe 1999). Isolated and fragmentary leaf remains like the Cretaceous fossils studied here can then be described and referred to without the complication of evolutionary considerations necessary when extrapolating back a name from a living plant. Palaeobotanists working on Antarctic leaves commonly use names such as *Dicotylophyllum* sp. 1, *Dicotylophyllum* sp. 2, etc., for form genera (e.g Birkenmajer and Zastawniak 1989a, Li 1994) in order to set up new species while affinities are uncertain. Cantrill and Nichols (1996) set up the form genera *Gnafalea* (an anagram of fagalean) for poorly preserved pinnately veined leaves of the Southern Hemisphere, describing two Albian species from Alexander Island. The anagram was used so that no botanical affinity was implied. One species *G. jeffersonii* was suggested to show affinities with the Hamamelidae or Dilleniidae, while the other, *G. binatus*, was described as a Rosid leaf form. Some of the most useful names, I believe, are those which give some indication of the leaf morphology and suggested botanical affinities. Examples include *Magnoliidaephyllum,* erected for leaves with characteristics typical of the Magnoliidae by Zastawniak (1994), and *Laurophyllum,* used by Pole (1993a) for Miocene leaves from New Zealand that lacked sufficient detail to be placed in modern genera of the Lauraceae.

Form genera are popular in palaeobotanical studies because various organs, such as leaves, pollen and wood, found separately can be given different names (Cleal 1986). These are considered provisional and can be altered at a later date when more information is available. For example, recovering cuticular anatomy or finding a leaf still attached to a branch with fruits or flowers would be an ideal situation. It may then be possible to assign the leaves to a natural genus.

Some palaeobotanical studies of the Antarctic Peninsula adopted the Hughesian taxonomic recording system. This replaces the traditional Linnean binomial names with a double-barrelled name that gives no indication of botanical affinities. Jefferson (1981) used this system for his research on fossil leaves and Chapman and Smellie (1992) named wood and pollen using this format. This type of approach would allow evolutionary studies based simply on morphology but is not favourable for rapid literature searches or communication of ideas. This type of system would be more beneficial if all fossil records, along with morphological characteristics, were stored in a data bank (see Chapter 4).

The approach followed in this study is similar to that adopted by many workers who use morphotypes to refer to a leaf form as a provisional measure until there is enough evidence to assign the leaves to an existing species or erect a new one. For example, Spicer (1986a, 1987) described his form system as a temporary "holding pattern" and Hill (1982) defined angiosperm leaf forms as parataxa, then following more detailed examination assigned some of the leaves to existing form genera (Hill 1986). Pole (1992, 1993a) also uses parataxa and names

consisting of an abbreviation of the locality and a specimen number. The term 'morphotype' used in this study refers to the list of architectural characters that defines a taxon or group of similar fossil leaf specimens. Morphotypes referring to morphological characteristics have been adopted by many researchers (e.g. Burnham 1986, Herman and Spicer 1997, Parrish *et al.* 1998). Crabtree (1987) used morphotypes carrying an implication of affinity in an appraisal of the Cretaceous angiosperm leaves of the Northern Rocky Mountains, including, for example, 'Platanophyll', which refers to leaves showing similarities to the Platanales, and 'Cinnamomophyll' for leaves with features characteristic of the Laurales. Zastawniak (1994) used these kinds of terms for Cretaceous angiosperm leaves from the Antarctic Peninsula to group leaves and then gave more detailed descriptions of particular form genera.

This discussion does not, however, rule out the assignment of modern generic or familial names to Late Cretaceous and early Tertiary angiosperm leaves. Detailed observations of well preserved fossil material and a thorough knowledge of the modern plant groups may allow relationships with extant genera to be established (Collinson 1986), especially if the fossil record is continuous. Identifications can also be supported with information from other plant parts such as pollen or wood. Although these leaves are provisionally named simply using a morphotype number, within each description there is a discussion of possible affinities (see Chapter 5). There are many cases where there is insufficient information to give more than a very general appreciation of possible affinities because of a lack of diagnostic characters. However, in other cases, possible affinities at the familial or generic level are suggested. For many of the morphotypes, confidence in these assignments is increased when arrived at independently and then shown to be supported by the occurrence of pollen or wood with the same possible affinities.

The following chapter describes attempts made to arrange these Cretaceous Antarctic dicotyledonous angiosperm leaves into distinct groups or taxa, which may then be compared with fossil and living plant groups. It presents the results of several different approaches to try and delineate morphotypes.

4   Approaches to grouping leaves as morphotypes

4.1 Introduction

This chapter describes attempts to classify the Late Cretaceous Antarctic angiosperm leaves in this project. Classification is the process of grouping things together on the basis of the features that they have in common. These distinct groups or taxa may then be compared with fossil and living plant groups. It is also necessary to summarise the data in this way so that it is possible to carry out further analyses, such as palaeoclimatic research.

This chapter presents the results of several different approaches to try and delineate morphotypes. Initial attempts included visual assessment of observed morphology (Section 4.2) and an artificial classification based on only one character (Section 4.3). However, angiosperm leaves of Cretaceous age demonstrate a high degree of morphological intergradation (Spicer 1986a,c, Thomas and Spicer 1987). There is considerable variation in size, shape and venation and these variations are so numerous and subtle that the leaves appear to form a morphological continuum. This makes it very difficult to formally classify fossil leaves of this age. These difficulties were encountered in this study of Cretaceous Antarctic angiosperm leaves. For this reason, it was found that a statistical approach was useful and the results are presented in Section 4.4.

4.2 Visual grouping based on common characters

Groups of individuals are intuitively recognised by shared characteristics. It became apparent from the drawings and descriptions that there were many leaves that were similar, suggesting that they belonged to the same group. The results from initial attempts to group the leaves visually, based on the descriptions and drawings, is presented below, but there were problems defining groupings. There are clearly different groups, but the variation suggests continuums between groups and there are no clearly defined boundaries.

Table 4.1 and Table 4.2 represent the subjective approach taking the general appearance of the leaves into account. The main features taken into account included shape, margins and venation patterns of the primary and secondary veins. Table 4.1 and Table 4.2 were constructed by simply visually assigning leaves to morphotype groups labelled A, B, C, etc. As is apparent from these tables, this was very difficult and resulted in large numbers of morphotype groups for both the Hidden Lake Formation and Santa Marta Formation floras. As can be seen from Table 4.1 and Table 4.2, large numbers of morphotypes with small numbers of specimens were grouped.

Table 4.1 Visually grouped morphotypes within the Hidden Lake Formation flora.

M	Specimen numbers
A	D8754.8.1a, D8754.8.2a&3a, D8754.8.58a, D8754.8.100a
B	D8754.8.4a&5a, D8754.8.4b&5b, D8754.8.4c, D8754.8.38a
C	D8754.8.4d, D8754.8.8b, D8754.8.49b
D	D8754.8.5d, D8754.8.26c, D8754.8.68a, D8754.8.76b, D8754.8.98d
E	D8754.8.6a
F	D8754.8.6b&65a, D8754.8.63a
G	D8754.8.7a
H	D8754.8.8a&9a
I	D8754.8.11b
J	D8754.8.14b
K	D8754.8.15a
L	D8754.8.16a
M	D8754.8.16b
N	D8754.8.16e
O	D8754.8.16f
P	D8754.8.17b
Q	D8754.8.17c
R	D8754.8.21a&46e
S	D8754.8.22a
T	D8754.8.22b
U	D8754.8.24b
V	D8754.8.25a
W	D8754.8.26a
	D8754.8.27a
X	D8754.8.28a
Y	D8754.8.30a
Z	D8754.8.31a
AA	D8754.8.32a&98e
AB	D8754.8.33a
AC	D8754.8.34a
AD	D8754.8.34b
AE	D8754.8.35a&37a
AF	D8754.8.36a
AG	D8754.8.39a

M	Specimen numbers
AH	D8754.8.39b
AI	D8754.8.40a
AJ	D8754.8.41a
AK	D8754.8.42a, D8754.8.45a, D8754.8.46a, D8754.8.98a
AL	D8754.8.43a
AM	D8754.8.44a, D8754.8.54a, D8754.8.57a
AN	D8754.8.44b
AO	D8754.8.45b, D8754.8.56b
AP	D8754.8.46d
AQ	D8754.8.47a
AR	D8754.8.47b
AS	D8754.8.48a
AT	D8754.8.48b
AU	D8754.8.49a
AV	D8754.8.50a
AW	D8754.8.50b
AX	D8754.8.54b
AY	D8754.8.58b
AZ	D8754.8.59a
BA	D8754.8.59c
BB	D8754.8.60a
BC	D8754.8.60b
BD	D8754.8.61a
BE	D8754.8.62a&64a
BF	D8754.8.66b
BG	D8754.8.67a
BH	D8754.8.67b
BI	D8754.8.71b
BJ	D8754.8.73b
BK	D8754.8.81b
BL	D8754.8.82b
BM	D8754.8.90b
BN	D8754.8.98b
BO	D8754.8.101a

Table 4.2 Visually grouped morphotypes within the Santa Marta Formation flora.

M	Specimen numbers
A	D8604.37A/Ca&37Ba, D8605.5a&15a, D8609.147a, DJ147.60b
B	D8604.38Aa&38Ba, DJ147.6a
C	D8604.39a, D8605.22Ba
D	D8604.54a, D8619.7a
E	D8605.1Aa&1Ba
F	D8605.2a
G	D8605.7a
H	D8605.8Aa&8Ba, DJ147.9a&15a, DJ147.60a
I	D8605.14a, D8610.1Aa&1Ba
J	D8605.16a
K	D8605.19Aa
L	D8605.20a
M	D8605.21Aa&21Ba
N	D8605.24a
O	D8605.26a
P	D8605.27Aa&Ba
Q	D8605.28a, DJ147.51a, DJ147.59a
R	D8605.29a
S	D8605.30a
T	D8605.31a
U	D8605.33a
V	D8606.4Aa&4Ba
W	D8606.5a
X	D8606.6a
Y	D8606.7Aa&7Ba, DJ134.15Aa&15Ba, DJ147.44a
Z	D8606.8a, D8616.128a, D8619.6a, DJ134.11a
AA	D8616.74a, D8625.119a, DJ134.13a
AB	D8618.106a
AC	D8619.12a
AD	D8619.18a
AE	D8621.27a
AF	DJ134.2Aa&2Ba, DJ147.24a
AG	DJ134.6a
AH	DJ134.12Aa&12Ba, DJ147.3a
AI	DJ134.16a, DJ452.2a
AJ	DJ134.21A/Ba

M	Specimen numbers
AK	DJ134.22A/Ba
AL	DJ134.27Ba
AM	DJ134.28a, DJ147.41Aa
AN	DJ147.1a
AO	DJ147.4a
AP	DJ147.7a
AQ	DJ147.8a
AR	DJ147.10a, DJ147.32a
AS	DJ147.11a
AT	DJ147.12Aa&12Ba, DJ147.46a
AU	DJ147.13a
AV	DJ147.14a
AW	DJ147.17a
AX	DJ147.18a
AY	DJ147.19a&54a, DJ147.38Aa&Ba, DJ147.56a
AZ	DJ147.20a
BA	DJ147.23a
BB	DJ147.25a, DJ147.40a
BC	DJ147.26a
BD	DJ147.28a
BE	DJ147.29a
BF	DJ147.30a
BG	DJ147.31a
BH	DJ147.33a
BI	DJ147.34a
BJ	DJ147.35a
BK	DJ147.37Aa&B/Ca
BL	DJ147.39a
BM	DJ147.43a
BN	DJ147.45a
BO	DJ147.48a
BP	DJ147.49Aa&Ba
BQ	DJ147.52a
BR	DJ147.53a
BS	DJ147.55Aa&Ba
BT	DJ451.7a

It was difficult to visually assess morphotypes because this involves considering many variables all at once. The poor preservation of the leaves also prohibits direct comparison of some of these variables. Visual grouping is notoriously difficult. For example, E. Kennedy (pers. comm.) demonstrated that given the same sample, different people grouped the same specimens into very different groups.

This is a very subjective approach, grouping leaves that look similar. It is difficult to do at this level of preservation and the result was a lot of different groups with a very small number of specimens in each group. This was unacceptable and of little value.

4.3 Grouping based on venation patterns

Since the above approach was not useful, it was decided to pick one significant variable to divide the leaves into groups. Cantrill and Nichols (1996) used venation as the main character for grouping mid-Cretaceous angiosperm leaves from the Antarctic Peninsula. They subsequently used these groups to define form genera.

Venation was a well preserved feature in many of the leaves studied here. Following the approach of Cantrill and Nichols (1996), the venation type was arbitrarily selected as the most important and leaves with a similar venation pattern were grouped together. Each leaf and its description was examined and categorised in terms of leaf venation (based on Hickey's scheme); the results are presented in Table 4.3 and Table 4.4.

Table 4.3 Grouping of Hidden Lake Formation flora based on venation patterns.

Morphotype	Specimen numbers
A (simple craspedodromous)	D8754.8.34a, D8754.8.46d, D8754.8.49b, D8754.8.6b&65a, D8754.8.8a&9a, D8754.8.101a
B (semicraspedodromous)	D8754.8.30a, D8754.8.31a
C (mixed craspedodromous)	D8754.8.28a
D (brochidodromous)	D8754.8.4b&5b, D8754.8.5d, D8754.8.15a, D8754.8.21a&46e, D8754.8.22b, D8754.8.26a, D8754.8.35&37a, D8754.8.36a, D8754.8.39a, D8754.8.42a, D8754.8.43a, D8754.8.45a, D8754.8.46a, D8754.8.48a, D8754.8.49a, D8754.8.98a, D8754.8.98c
E (eucamptodromous)	D8754.8.33a, D8754.8.40a, D8754.8.41a, D8754.8.63a
F (reticulodromous)	
G (acrodromous)	D8754.8.16b, D8754.8.44a, D8754.8.54a, D8754.8.57a, D8754.8.60a, D8754.8.67b
H (actinodromous)	D8754.8.1a, D8754.8.2a&3a, D8754.8.4a&5a, D8754.8.4c, D8754.8.61a, D8754.8.100a
I (palinactinodromous)	D8754.8.62a&64a
Unclassifiable	D8754.8.6a, D8754.8.7a, D8754.8.8b, D8754.8.11b, D8754.8.14b, D8754.8.16a, D8754.8.16e, D8754.8.16f, D8754.8.17b, D8754.8.17c, D8754.8.22a, D8754.8.24b, D8754.8.25a, D8754.8.26c, D8754.8.27a, D8754.8.32a&98e, D8754.8.34b, D8754.8.38a, D8754.8.38b, D8754.8.39b, D8754.8.44b, D8754.8.45b, D8754.8.47a, D8754.8.47b, D8754.8.47c, D8754.8.48b, D8754.8.49c, D8754.8.4d, D8754.8.50a, D8754.8.50b, D8754.8.54b, D8754.8.56b, D8754.8.58a, D8754.8.58b, D8754.8.59a, D8754.8.59c, D8754.8.60b, D8754.8.66b, D8754.8.67a, D8754.8.68a, D8754.8.68b, D8754.8.71b, D8754.8.71c, D8754.8.73b, D8754.8.76b, D8754.8.81b, D8754.8.82b, D8754.8.90b, D8754.8.98b, D8754.8.98d

Table 4.4 Grouping of Santa Marta Formation flora based on venation patterns.

Morphotype	Specimen numbers
A (simple craspedodromous)	D8605.19Aa, D8606.5a, D8606.6a, D8616.74a, D8616.128a, D8619.6a, D8621.27a, D8625.119a, DJ134.13a, DJ134.22A/Ba, DJ147.35a, DJ147.51a
B (semicraspedodromous)	D8606.7Aa&7Ba, DJ134.15Aa&Ba, DJ134.2Aa&Ba, DJ134.28a, DJ147.24a, DJ147.41Aa, DJ147.44a, DJ147.55Aa&Ba
C (mixed craspedodromous)	
D (brochidodromous)	D8604.37A/Ca&Ba, D8604.54a, D8605.1Aa&1Ba, D8605.2a, D8605.21Aa&Ba, D8605.30a, D8609.147a, D8618.106a, D8619.7a, D8619.18a, DJ134.27Ba, DJ147.9a&15a, DJ147.10a, DJ147.12Aa&Ba, DJ147.14a, DJ147.19a&54a, DJ147.25a, DJ147.31a, DJ147.32a, DJ147.33a, DJ147.37Aa&B/Ca, DJ147.38Aa&Ba, DJ147.39a, DJ147.40a, DJ147.46a, DJ147.56a,
E (eucamptodromous)	D8610.1Aa&Ba, DJ134.16a, DJ451.7a
F (reticulodromous)	D8604.38Aa&Ba, D8605.31a, DJ147.6a
G (acrodromous)	D8605.33a, DJ134.6a, DJ147.4a, DJ147.30a
H (actinodromous)	DJ147.11a, DJ147.20a, DJ147.49Aa&Ba, DJ147.53a
I (palinactinodromous)	D8619.12a, DJ134.21A/Ba
Unclassifiable	D8604.39a, D8605.5a&15a, D8605.7a, D8605.8Aa&Ba, D8605.14a, D8605.16a, D8605.20a, D8605.22Ba, D8605.24a, D8605.26a, D8605.27Aa&Ba, D8605.28a, D8605.29a, D8606.4Aa&Ba, D8606.8a, DJ134.11a, DJ134.12Aa&Ba, DJ147.1a, DJ147.3a, DJ147.7a, DJ147.8a, DJ147.13a, DJ147.17a, DJ147.18a, DJ147.23a, DJ147.26a, DJ147.28a, DJ147.29a, DJ147.34a, DJ147.43a, DJ147.45a, DJ147.48a, DJ147.52a, DJ147.59a, DJ147.60a, DJ147.60b, DJ452.2a

This approach was more productive. A smaller number of groups were produced with some confidence. However, there were problems experienced when attempting to define leaves using venation type. Firstly, assigning the venation type is difficult, which is one of the reasons newer classification schemes have been proposed for leaf architecture (see Chapter 3). For example, the distinction between pinnate camptodromous brochidodromous and pinnate camptodromous eucamptodromous venation is not always clear, especially when studying fossil leaves. Secondly, once separated into these groups, despite having similar venation patterns, there is an unacceptably wide variation of other features, such as margin styles, within each group. For example, group G (Table 4.3) includes leaves with very different shapes and margin styles. The groups contain such a wide variety of features that a lot of information is lost. Visually each group appeared to contain several distinct taxa, but it was not clear on which character to further subdivide each group.

The problem with this method of grouping is that whilst many visual characters are recorded, there still has to be a subjective assessment of the most important features as a basis for grouping. This approach requires a decision on a hierarchy of characters, giving the most weight to one arbitrarily selected character, and then selecting another to further subdivide the groups produced. The features of leaf architecture outlined in Chapter 3 have all been shown to be useful in identifying dicotyledonous angiosperm leaf groups (Hickey 1973, 1979; Hickey and Wolfe 1975), but there is no clear hierarchical key of characters.

These groups based on venation pattern alone could not be compared with fossil or living families, genera or species because the venation pattern used to define each group is common to many different dicotyledonous angiosperm groups. Looking at venation in modern leaves alone, it is clear that one venation type is seen in widely different dicotyledonous groups (some considered not closely related). For example, acrodromous venation is common to many plant orders within the Magnoliidae (Laurales, Piperales, Aristolochiales), Hamamelidae (Urticales)

and Dilleniidae (Myrtales, Malvales) (Hickey and Wolfe 1975). There is also a wide variation of venation types observed within one living angiosperm leaf family, e.g. the leaves of living Lauraceae may be brochidodromous, eucamptodromous, or acrodromous. Venation patterns, along with marginal features, are especially valuable in identification, but a set of characters useful for recognising one taxon may be completely different from those distinguishing another (Hickey 1973, 1979).

The principal problem with this approach, however, is the significant number of these Cretaceous Antarctic leaf specimens that are too fragmentary to allow the venation pattern to be categorised with certainty. What should be done with these? It is important not to ignore the less well preserved fragmentary specimens within these floras. The lack of facies more suitable for preservation in the Cretaceous of the Southern Hemisphere, along with the comparative inaccessibility of Antarctic regions, means that floral and palaeoclimate reconstructions rely on relatively small collections and fragmentary material. Merely assigning them as unclassifiable would eliminate a large element of the diversity of the angiosperm floras from the study. Many researchers (e.g. Spicer 1989, 1990a, Wolfe 1993) have also asserted that the study of the most fragmentary elements of an assemblage is crucial in order to account for taphonomic biases when making interpretations of past temperatures and precipitation.

Table 3.1 clearly illustrates the point that there is not one single character preserved in all, or at least most, of the leaf fossils on which grouping can be initiated. It was for this reason that a multivariate statistical approach was attempted. This allows more than one leaf character to be used simultaneously in classification. Although each leaf fragment preserves a subset of the different features considered useful in systematic studies of dicotyledonous angiosperm leaves, it was hoped that using many characters and measurements would allow a valid assessment of overall similarities and differences.

4.4 Statistical approach

4.4.1 Introduction

It is apparent from the discussion above that to clearly define a fossil leaf taxon it is preferable to take the architecture as a whole into account. Since there is no well-defined grouping on venation alone, the principles of phenetics and multivariate statistical methods were used to cluster the leaves using as many characters as could be measured. These included types of leaf shape, the style of the apex and base, angles, marginal features, and primary, secondary, and tertiary venation patterns.

Phenetics is defined as grouping by overall or aggregate similarity and is a pattern of classification that can be used to generate a dichotomous dendrogram. This technique involves the recording of all available characters, assigning them equal weighting and using them to create groups of similar leaves. Clustering of individuals into species and taxa of higher rank is an agglomerative rather than a divisive process. Aggregate similarities or differences among

taxa are represented as distances in character hyperspace, and thus clusters are formed. This is claimed to be a more objective approach than traditional division of organisms into taxa (Sneath and Sokal 1973, Dolph 1975, 1976, Panchen 1992, Hall 1997).

A very early example of this type of approach is a two-dimensional clustering of the plant kingdom drawn by Giseke (1792) from the work of Linnaeus (in Panchen 1992) (Figure 4.1). The diagram is an arrangement of large and small circles, each representing a taxon, in the same way that modern numerical taxonomy envisages taxa in hyperspace. Adanson, a contemporary of Linnaeus, produced 65 rival classifications, each based on the states of a different character, which he compared against his natural families, aiming to show the futility of artificial classifications based on one or a few characters (Sokal and Sneath 1963). Several workers including Sneath and Sokal developed the modern method of phenetic classification and numerical taxonomy in the 1950s and 1960s. The theory and methods in phenetics are outlined in Sneath and Sokal (1973).
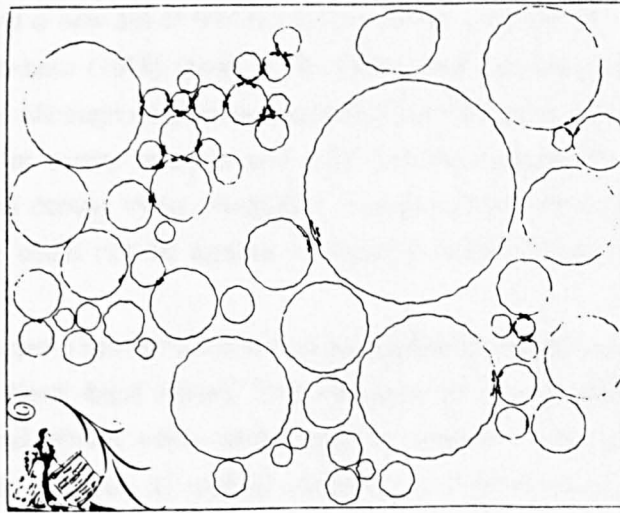
Figure 4.1 A two-dimensional clustering of the Vegetable Kingdom by PD Giseke (in Linnaeus 1792), in which each circle represents a plant group. (Edited from Panchen 1992.)

Statistical methods used previously by palaeobotanists to isolate groups of dicotyledonous angiosperm leaves include Hill's (1982) study of Eocene fossils from Australia and an analysis of Eocene material from North America by Dolph (1975). Dolph (1976) and Hill (1980a) analysed living specimens of known identification to assess the validity of using their character sets to partition a collection of unknown specimens into leaf types. These statistical methods were also developed to determine whether it would be possible to construct a computer data bank of leaf characters from fossil and living taxa to aid in the identification of fossil dicotyledonous leaves. A statistical approach using rigorously defined characters to compare a specimen with known species is considered more objective than traditional subjective decisions on species affinities (Dolph 1976).

Although the numerical taxonomic methods of Dolph (1976) and Hill (1980a) have been successful in partitioning living angiosperm leaf taxa, clustering leaves of the same species

together, neither was suitable for this study of Antarctic Cretaceous fossils. The reasons these methods could not be used are outlined in the brief summaries of these approaches below.

Dolph's (1976) approach was initially favoured because it is based on the Hickey (1973, 1979) character set, the scheme selected for this study of Cretaceous leaves in order to facilitate comparison with other studies of dicotyledonous angiosperms (see Chapter 3). The partitioning method is based on binary and multistate qualitative characters (explained in Table 4.5) of leaf architecture. However, this method could not be applied in its original form because many of the characters required were not preserved in a significant number of these Antarctic Cretaceous leaves, e.g. gland position and features of the higher order venation, such as veinlet type and areole development. Furthermore, Hill (1980a) considered that the recognition of higher vein orders was unreliable in fossil specimens and that these should not be used as primary characters in numerical taxonomy.

Hill (1980a) compiled a new set of continuous characters modified from character lists for leaf architecture by Blackburn (1978) (cited in Hill 1980a) and cuticular anatomy by Stace (1965) (cited in Hill 1980a). Although continuous characters take longer to score, it was proposed that these were better for cluster analysis and data banking because they allow more rigorous statistical testing and convey more information. However, there were several reasons why this particular approach could not be applied to these Antarctic Cretaceous leaves. These are outlined below:

- Hill (1980a) erected a new scheme for the recognition of different vein orders that could not be applied to these fossil leaves. The definition of primary veins does not recognise suprabasal lateral primary veins, which were not present in Hill's study, but are present in these floras (Morphotypes 31 and 32, Chapter 5). The principal problem, though, is the definition of secondary veins. Rather than vein width and behaviour, their recognition relies on the measurement of the length of all the secondary veins of each leaf. This was not generally possible for these fragmentary Cretaceous specimens.

- Ten of the 31 characters used are based on cuticular anatomy, which is not preserved in these Cretaceous fossils.

- Of the remaining leaf architectural characters, very few can be applied to the fragmentary fossils studied here. Many rely on the accurate measurement of the leaf outline (e.g. length, width, leaf-shape index), and most of the other characters require the presence of the full length or width of the leaf for their definition (e.g. basal angle, number of secondary veins, secondary vein straightness index). There are also several characters based on higher order venation (e.g. number of veinlets per areole), which, as stated above, is insufficiently preserved in the Cretaceous leaves.

Recognising that the characters of cuticle and higher order venation are unlikely to be preserved in most fossil material and that a high proportion of the remaining architectural characters rely on the full length of the leaf being preserved, Hill (1980a) defined modified leaf length to account for incomplete leaves. This involves the recognition of intercepts of the leaf margin with

lines at 10°, 170°, 190° and 350° with respect to the midvein. Most of the Antarctic Cretaceous leaves were still too fragmentary to be measured in this way and Hill clearly states that if the 10° lines do not intercept the margin because too much of the leaf is missing, then the leaf is too incomplete for his approach to be applied.

For the present study, recommendations from both these approaches were considered and a combination of the two methods was constructed. Whilst learning to apply this multivariate technique and becoming familiar with the computer software, the method was initially developed using leaves from living species. Observations from herbarium material and photographs of modern leaves of known identification were used and these initial trials gave promising results, clustering leaves of the same family together.

4.4.2 Stages within a numerical taxonomic approach

There are a series of stages in a numerical taxonomic study, summarised below.
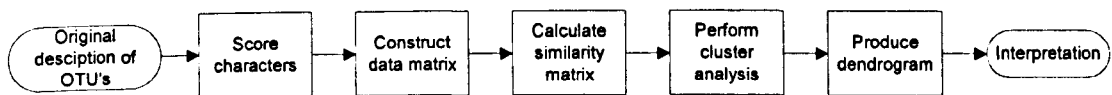
4.4.2.1 Original study of OTUs

The first stage is the original study of the specimens or 'Operational Taxonomic Units' (OTUs). Each OTU is referred to using leaf specimen numbers (listed in Appendix 2, Table A2-1 and A2-2). The specimens are described in terms of a series of characters. The terminology used in this study is discussed in Chapter 3 and the original descriptions of these Cretaceous Antarctic angiosperm leaves from which the specific characters are taken are given in Appendix Volume 2.

4.4.2.2 Character scoring and construction of data matrix

These descriptions must then be converted into a format that can be entered into a data matrix. A data matrix is a table in which OTUs are ranged down the side, with the characters studied along the top. Each OTU is characterised by the state of each character and scored accordingly. States of all the characters are then recorded in the cells of the matrix.

The character scoring for this study is based on the characters defined by Hickey (1979), outlined in Chapter 3, and adapted from the methods of Dolph (1976) and Hill (1980a), described in Section 4.4.1. These characters are based on features of lamina symmetry, form, margin type, presence of a petiole, venation type, primary vein size and course, secondary vein divergence angles and courses, presence of intersecondary veins, outer secondary veins or an intramarginal vein, and tertiary vein angles.

It is only acceptable to use primary characters in numerical taxonomic studies (Sneath and Sokal 1973, Dolph 1976). These are characters that could occur in all of the leaves (if they were completely preserved), e.g. margin type. The tooth type, however, cannot be used. This is an example of a secondary character, only present in those leaves with toothed margins. Inclusion of this type of character would cause problems because there can be no comparisons when leaves with smooth margins are considered. Ultimately, 23 characters were used in this study of Late Cretaceous angiosperm leaves, less than the character set of Hill (1980a), but greater than that of Dolph (1976). Hill's numerical methods were also successful when based on only 14 leaf architectural characters.

There are different types of characters used in numerical taxonomic studies and these are explained in Table 4.5.

Character	Definition	Examples from angiosperm leaf studies
Binary	Two-state characters	Lamina - symmetrical or asymmetrical
	Presence-absence characters	Petiole - present or absent
Multistate	Qualitative discrete states	Leaf apex form – acute, attenuate, or obtuse
Continuous quantitative	Direct measurement of a continuum	Secondary vein divergence angle - 45°, 57°
Meristic quantitative	States form a series of discrete numbers	Number of secondary veins – 8, 9 or 10

Table 4.5 Types of characters used in numerical taxonomic studies. These definitions are taken from Sneath and Sokal (1973) and Panchen (1992).

Meristic quantitative characters are not used in this study and are not further considered.

4.4.2.2.1 Initial attempts – binary character coding

Because of the limitations of the software available, initial attempts at designing a character scoring method were restricted to binary format. Binary characters are two-state or presence-absence characters.

OTU	Intersecondary veins
D8754.8.1a	0
D8754.8.8a&9a	1

Table 4.6 An example of binary coding.

Coding of characters is simple if the states are present or absent, e.g. presence (1) or absence (0) of intersecondary veins. For example, in Table 4.6, OTU D8754.8a&9a has intersecondary veins present, while they are absent in D8754.8.1a. All two-state characters, however, can also be arbitrarily coded 0 or 1. For example, lamina symmetry may be symmetrical or asymmetrical. As discussed in Chapter 3, the confident definition of symmetry in fragmentary leaves is difficult. When a leaf is incomplete, it is only really possible to recognise asymmetry. A fragmentary leaf may appear symmetrical, but without the whole leaf preserved this cannot be certain. Since it was believed that this character would therefore reflect presence of asymmetry, symmetrical

leaves were scored as 0 and asymmetrical leaves as 1. Characters of this type used in this study are listed in Table 4.7. Dolph (1976) uses characters 1, 2, 3, 15, and 19 similarly. Dolph (1976) did not use presence or absence of petiole because it was invariant in his study sample, but was considered useful in this study, along with other new characters from Hickey's scheme, e.g. presence of an intramarginal vein. These characters are considered useful in systematic studies by Hickey and their usefulness was established during initial trials on modern leaves of known identification.

Character Number	Character	Type	Character State
1	Lamina symmetry	B	0=symmetrical 1=asymmetrical
2	Basal symmetry	B	0=symmetrical 1=asymmetrical
3	Apical symmetry	B	0=symmetrical 1=asymmetrical
8	Petiole	B	0=absent 1=present
15	Symmetry of secondary vein divergence	B	0=symmetrical 1=asymmetrical
17	Secondary vein branching	B	0=unbranched 1=branched
18	Outer secondary veins	B	0=absent 1=present
19	Intersecondary veins	B	0=absent 1=present
20	Intramarginal vein	B	0=absent 1=present

Table 4.7 Binary characters used in this study of Antarctic angiosperm leaves.

Binary coding of other types of characters which have more than two states, e.g. leaf form, or are quantitative measurements, e.g. secondary vein divergence angle, is more difficult. Although it was desirable to enter the actual state or measurement on the data matrix, the clustering method and computer program first used demanded binary coding. First attempts at scoring the characters in this study therefore involved converting all the characters so that they could be scored as binary states.

OTU	Pinnate simple craspedodromous	Pinnate semicraspedodromous	Pinnate mixed craspedodromous	Pinnate brochidodromous	Pinnate eucamptodromous	Pinnate reticulodromous	Acrodromous	Actinodromous	Palinactinodromous
D8754.8.1a	0	0	0	0	0	0	0	1	0
D8754.8.8a&9a	1	0	0	0	0	0	0	0	0
D8754.8.57a	0	0	0	0	0	0	1	0	0
DJ147.46a	0	0	0	1	0	0	0	0	0

Table 4.8 An example of binary coding for a qualitative multistate character 'venation type' using nine binary characters.

Table 4.8 is an example illustrating an initial attempt to convert qualitative multistate characters to binary format. In this example of binary coding of venation type it can be seen that D8754.8.1a has actinodromous venation and DJ147.46a has pinnate brochidodromous venation.

It was also attempted to convert continuous quantitative characters to binary format in the same way. For example, the character 'secondary vein divergence angle' was broken up into a series of unit characters with two states using category limits from Hickey (1979). These limits are narrow acute (<45°), moderate acute (45-65°), wide acute (65-80°), approximately right-angled (80-100°), and obtuse (>100°). In the example in Table 4.9, D8754.8.1a has a wide acute angle of secondary divergence, while D8754.8.8a&9a and DJ147.46a have a moderate acute angle.

OTU	Narrow acute	Moderate acute	Wide acute	Right-angled	Obtuse
D8754.8.8a&9a	0	1	0	0	0
D8754.8.1a	0	0	1	0	0
DJ147.46a	0	1	0	0	0

Table 4.9 An example of binary coding for a continuous character 'secondary vein divergence angle' using five binary characters.

However, it was concluded that this approach was unsatisfactory. The problem with this sort of binary coding of multistate and continuous characters is the logical correlation of the character states. For example, the recording of the character 'actinodromous venation' as present for an OTU automatically brings about absent scores on all the other characters derived from the qualitative character 'venation pattern', making these eight characters redundant. This would apply to all multistate or continuous characters scored for these Cretaceous angiosperm leaves using the binary format described above (e.g. apex form, primary vein size). Sneath and Sokal (1973) considered that this method of using series of binary characters is only applicable where it is evident that the new characters are logically independent and could theoretically occur in any combination, but this is not the case here. For example, one fossil leaf specimen can never have an apex that is both obtuse and attenuate.

This binary scoring was unacceptable and it was necessary to combine different types of characters in order to represent the fossil leaf specimens in a data bank.

4.4.2.2.2 Character scoring of Cretaceous Antarctic angiosperm leaves

The list of characters used in this study and the method of scoring is shown in Table 4.10. The challenge presented was to find a suitable statistical method and computer software package for dealing with the combination of binary, multistate and continuous characters. The solution is discussed at the end of this section and in Section 4.4.2.3.

Character number	Character	Type	Character State
1	Lamina symmetry	B	0=symmetrical 1=asymmetrical
2	Basal symmetry	B	0=symmetrical 1=asymmetrical
3	Apical symmetry	B	0=symmetrical 1=asymmetrical
4	Lamina form	M	1=oblong 2=elliptic 3=ovate 4=obovate
5	Apex form	M	1=acute 2=acuminate 3=attenuate 4=obtuse 5=emarginate 6=truncate
6	Base form	M	1=acute-normal 2=acute-cuneate 3=acute-decurrent 4=obtuse-normal 5=obtuse-cuneate 6=rounded 7=cordate 8=lobate 9=hastate
7	Margin type	M	1=entire 2=lobed 3=toothed 4=crenate 5=erose
8	Petiole	B	0=absent 1=present
9	Venation type	M	1=pinnate simple craspedodromous 2=pinnate semicraspedodromous 3=pinnate mixed craspedodromous 4=pinnate brochidodromous 5=pinnate eucamptodromous 6=pinnate reticulodromous 7=acrodromous 8=actinodromous 9=palinactinodromous

Character number	Character	Type	Character State
10	1° vein size	M	1=massive 2=stout 3=moderate 4=weak
11	1° vein course	M	1=straight 2=curved
12	2° vein divergence angle	Q	
13	Basal 2° angle	Q	
14	Variation in 2° vein divergence	M	1=nearly uniform 2=upper 2°s more obtuse than lower 3=upper 2°s more acute than lower 4=lowest pair more acute than all others 5=lower and upper 2°s more obtuse than middle sets 6=irregular
15	Symmetry of 2° vein divergence	B	0=symmetrical 1=asymmetrical
16	Course of 2° veins	M	1=straight 2=recurved 3=curved 4=sinuous
17	2° vein branching	B	0=unbranched 1=branched
18	Outer 2° veins	B	0=absent 1=present
19	Intersecondary veins	B	0=absent 1=present
20	Intramarginal vein	B	0=absent 1=present
21	Admedial 3° vein angle	Q	
22	Exmedial 3° vein angle	Q	
23	Midvein 3° vein angle	Q	

Table 4.10 Character scoring devised for these Cretaceous Antarctic dicotyledonous angiosperm leaves. B – binary characters; M – multistate characters; Q – continuous quantitative characters.

In addition to the nine binary and two-state characters described in Section 4.4.2.2.1, there are nine multistate characters and five continuous quantitative characters.

Three multistate characters 'primary vein size', 'variation in secondary vein divergence', and 'secondary vein course' are as used by Dolph (1976). Three other multistate characters are similar to those used in Dolph's scoring scheme except that states are omitted because they are not present in these Cretaceous Antarctic leaves (see Table 3.1 summarising characters observed in these floras). These characters include 'apex form' (reduced from 9 to 6 states), 'primary vein course' (reduced from 4 to 2 states), and 'base form' (reduced from 14 to 9 states). The character states omitted from the character 'base form' included categories from Hickey's scheme and the new states added by Dolph, which were not observed in these leaf floras. Character states omitted could easily be added if new leaf material meant that it became necessary.

Three of the multistate characters were used as set out by Hickey (1973, 1979) without Dolph's modifications. The 'lamina form' character retained the same states as Hickey's scheme because the various lobed character states added by Dolph (1976) were not observed in these Cretaceous leaves. The character 'margin type' is therefore also different because lobes are retained as marginal features (as in Hickey's original scheme). Other margin character states 'dentate' and 'serrate' were combined as 'toothed' because of the difficulties in distinguishing between the two tooth types in fossil specimens. There is actually only one poorly preserved morphotype (Morphotype 6, Chapter 5) within these Cretaceous floras with a dentate margin. The margin character state 'crenate' from Hickey's scheme was also not used in Dolph's coding but was necessary in this study, and since 'revolute' margins were not confidently recognised this state was omitted. The character 'venation type' was also used as set out by Hickey (1979) with a reduced number of states (9 compared to the 14 used by Dolph). Four of these were states from Hickey's scheme that were not observed in the Cretaceous leaves, e.g. 'campylodromous venation'. The fifth omission was the character state added by Dolph, 'intramarginal'. Leaves with intramarginal veins are categorised under the brochidodromous venation type (Hickey 1973, 1979, Hickey and Wolfe 1975) and in this study the presence or absence of an intramarginal vein is included as a separate binary character (see Section 4.4.2.2.1).

The combination of multistate characters used in describing leaf form was considered very useful in this study of Cretaceous angiosperm leaves. Quantitative measurements of lengths, ratios and angles, such as those set out by Hill (1980a), could not be applied because of the fragmentary nature of the material. Using qualitative characters for these predominantly incomplete leaves it was possible to clearly determine which of the qualitative categories used the lamina, apex, or base form, for example, should fit into.

The five remaining continuous characters are quantitative measurements of angles, 'secondary vein divergence angle', 'basal secondary vein divergence angle', 'admedial tertiary vein angle',

'exmedial tertiary vein angle', and 'midvein tertiary vein angle'. These characters refer to the average angles, measured as set out by Hickey (1979) (see Chapter 3, Appendix 1). The characters used are different to those set out by Dolph (1976), in which no characters are based on tertiary venation, and are influenced by the scheme of Hill (1980a). For quantitative coding of vein angles, Hill (1980a) only measured one tertiary vein on either side of the midvein. In this study of Cretaceous leaves, however, many angles (up to 80) were measured and an average was taken to reduce possible errors in the incorrect recognition of a feature of the fossil as a vein.

Secondary vein divergence was considered very important in this study of Antarctic leaves because, as can be seen from Figure 4.3 and Table 3.1, this is one of the most consistently preserved features. It is clear from the classification schemes of Hickey (1973, 1979), Dolph (1976), and Hill (1980a) that the secondary vein divergence angle may vary over the length of the lamina. Therefore, when studying fragmentary specimens, it is not possible to directly compare the average secondary vein divergence angle measured from an apical leaf fragment with the average secondary vein divergence measured from a basal leaf fragment. To facilitate comparison between leaves of variable completeness, it was decided that the only veins included in the coding of average secondary vein divergence should be those from the middle part of the leaf. This also eliminates the problem of the rather subjective recognition of relatively fine secondary veins near leaf apices, which was one of the reasons for the rigorous method of identifying secondary veins proposed by Hill (1980a). In this study of Cretaceous leaves, the 'basal secondary vein angle' is created as a separate character. The basal pair of secondary veins has been observed to frequently diverge from the midvein at a markedly different angle to the secondaries above (Hill 1980a). Tertiary vein divergence angles may also vary over the length of the lamina and so the apical and basal parts of the leaves were also excluded when measuring tertiary vein divergence angles.

In Dolph's coding scheme, secondary vein divergence angle is coded as a multistate character using the boundaries defined by Hickey (1973, 1979), narrow acute, moderate acute, wide acute, right-angled, and obtuse. However, there are no leaves with secondary veins (including basal secondary veins) diverging at an obtuse angle from the midvein and a right-angled secondary vein divergence is very rare (Table 3.1). The majority of leaves studied here have a moderate acute angle of secondary vein divergence (45-65°) and narrow acute basal secondary vein divergence (<45°). Tertiary vein divergence angles are also consistently well preserved in these Cretaceous floras and again obtuse angles of tertiary vein origin are rare. Dolph (1976) had concluded that the qualitative characters he used were insufficient and following Hill (1980a) and Hall (1997), it was considered that more discriminatory power would be given to these well preserved features if continuous quantitative characters were used.

The resulting combination of binary, multistate, and continuous characters used in this study of angiosperm leaves presented problems in finding suitable statistical methods and computer software. The computing solution was found in MVSP (Kovach Computing Services). This

package allows the declaration of character type in the label for each variable. Those beginning with 'b_' are taken to be binary, those with 'm_', multistate, and anything else is considered quantitative. Using their example, a variable indicating the presence or absence of sepals in a flower would have the label 'b_sepal', that indicating the colour of the petals (one of four possible) would be named 'm_colour', and petal length would be recorded in the row with the label 'length'.

The data matrices containing all the coding for the Hidden Lake Formation flora and the Santa Marta Formation flora are given in Appendix 3, Tables A3-1 and A3-2.

4.4.2.2.3 Missing data

It is apparent from the data matrices for both floras (Appendix 3, Table A3-1 and A3-2) that there is a considerable amount of missing data ('nc' – no comparison). Figure 4.2 is a representation of the amount of missing data within these Cretaceous Antarctic floras, illustrating the total number of characters present in the leaves. There are only four leaves with all 23 characters present and in eleven leaves only one character can be clearly observed. In the majority of specimens, 10 to 21 of the 23 characters can be described.
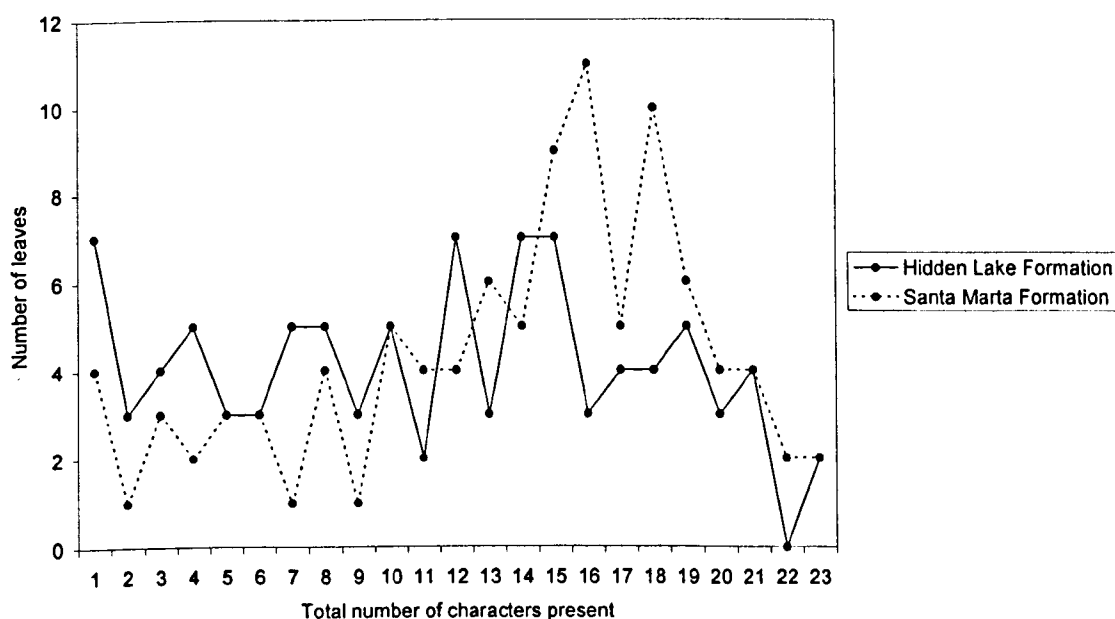
Figure 4.2 Total number of characters present in the Hidden Lake Formation and Santa Marta Formation leaves. (HLF n=94, SMF n=99).

Taking each of the 23 characters separately, Figure 4.3 shows the percentage of leaves in which that character is missing. The least often preserved characters are those relating to lamina symmetry and shape and the most frequently preserved are those relating to the margins and the primary, secondary and tertiary veins.
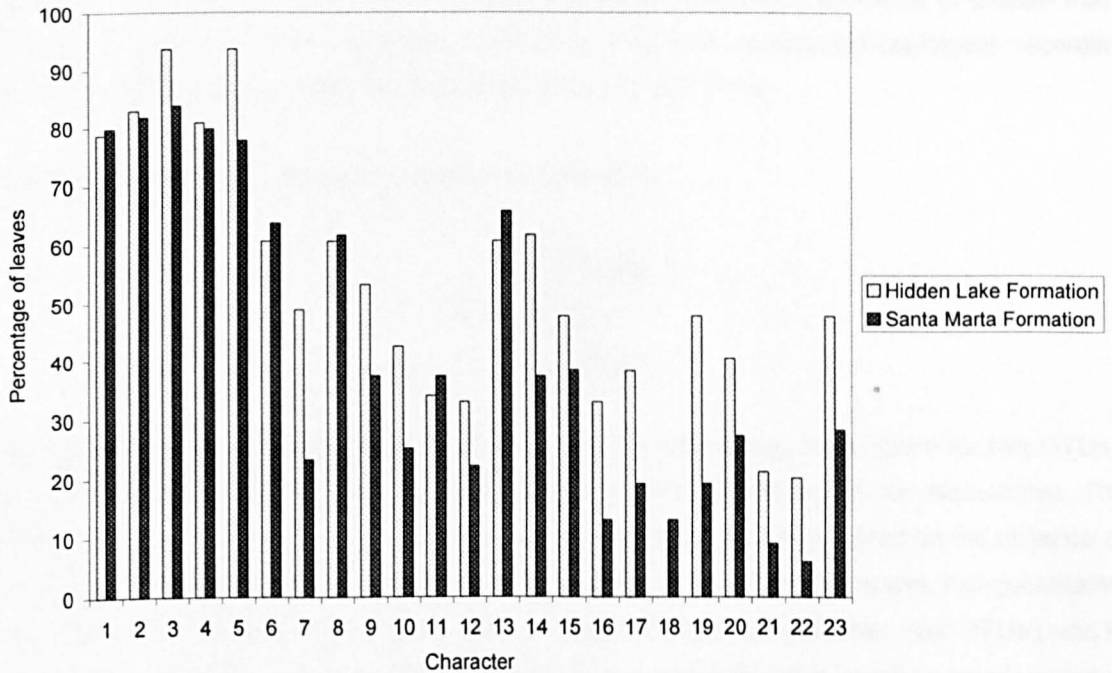
Figure 4.3 The proportion of missing data for each of the 23 characters used in this study of the Hidden Lake Formation and Santa Marta Formation floras. (HLF n=94, SMF n=99).

The total amount of missing data is considered high (compare Hill 1980a). The Hidden Lake Formation flora has 1111 missing variables out of a possible 2162 scores (51%) and the Santa Marta Formation flora has 941 missing variables out of a possible 2277 (41%). When the data matrix is imported into MVSP, this non-numerical data is converted to zero. For the numerical analysis used, this is acceptable for binary and multistate characters. However, if quantitative characters, with a majority of values between about 70 and 100, were scored zero for missing data, the resulting high variance would have an unjustifiably great effect on the clustering analysis. This problem was overcome by using averages for the missing values of quantitative characters. For example, for the character 'secondary vein divergence angle', the average value is 57, and this figure was substituted for all the OTUs with missing values for that character. The data matrix could then be imported into MVSP.

4.4.2.3 Production of a similarity matrix

Once the coding of the data matrix is complete, the next stage is the production of a similarity matrix, created by comparing every OTU pairwise with every other OTU. The OTUs are listed along each axis of the matrix and the cells record a measure of similarity. The similarity between two OTUs is estimated by means of a similarity coefficient, which is a quantification of resemblance based on all the character states of the two OTUs in question.

In order to deal with the range of binary, multistate, and continuous characters used in this study of Cretaceous Antarctic leaf specimens, the similarity coefficient selected was the General Similarity Coefficient of Gower (Gower 1971, Sneath and Sokal 1973). MVSP was especially

useful for this study because there is a wide selection of similarity coefficients to choose from, including the Gower General Similarity Coefficient. This is an association coefficient, recording matches and mismatches between all the characters of two OTUs.

The General Similarity Coefficient of Gower is defined as:

$$S_G = \frac{\left(\sum_{i=1}^{n} w_{ijk} S_{ijk}\right)}{\sum_{i=1}^{n} w_{ijk}}$$

For each character, i, a score, S_{ijk}, from 0 to 1, and a weight, w_{ijk}, is assigned for two OTUs **j** and **k**. Binary and multistate characters are scored 1 for matches and 0 for mismatches. The weight is set to 1 for matches, and to eliminate spurious high similarity based on the absence of features, the weight is set to 0 for negative (0) matches of two-state characters. For quantitative characters $S_{ijk} = 1-(|X_{ij}-X_{ik}|/R_i)$, where X_{ij} and X_{ik} are the scores of character i for OTUs **j** and **k**, and R_i is the range of character i in the sample. Continuous characters are thus standardised to between 1, when character states are identical, and 0, when two character states span the extremes of the range of the character.

The General Similarity Coefficient of Gower was selected because it is able to cope with the mixture of binary, multistate and continuous characters scored in this study. It is considered to be one of the most straightforward coefficients suitable for use with the type of data obtained in this study of angiosperm leaves (M. Wills pers. comm., Sneath and Sokal 1973) and it has been previously used in taxonomic studies (e.g. Sheals 1964, Sims 1966).

From the input data matrix of variously coded characters, using this coefficient, the computer program calculates a similarity matrix.

4.4.2.4 Phenetic clustering and production of a dendrogram

Clustering in phenetics is agglomerative, starting with individuals and clustering them into successively larger groups (Sokal and Sneath 1963, Shi 1993). The method of clustering used in this study is the 'unweighted pair-group method using arithmetic averages' (UPGMA), which is the most commonly used approach (Sokal 1986). Dolph (1976) tested various clustering algorithms and found that UPGMA consistently gave the best results. This method was also successful in Hill's (1980a) study of modern leaves of known identification, clustering OTUs into species. The clustering begins with distinct OTUs and unites the pair of OTUs with the greatest similarity coefficient. That pair is then represented by a single taxon, which replaces them in the similarity matrix. Then the next closest pair is joined and the procedure is continued sequentially until all the OTUs have been included (Sneath and Sokal 1973, Panchen 1992). The results of this hierarchic technique are represented by a dichotomous dendrogram, or phenogram, in which the nodes represent all the characters shared by their dependent branches and the OTUs

at the ends of the branches. The horizontal distances between node and OTU, or between node and node, are measures of similarity. Two OTUs that are closely similar have short branches to the node that exclusively unites them, while longer branches join OTUs that are less similar.

4.4.2.5 Interpreting the dendrogram

The results of the clustering procedure are presented in Section 4.4.3. There have been several methods proposed for defining groups or taxa once the dendrogram has been generated. One method involves the use of 'phenons', vertical lines drawn across the dendrogram at various levels of percentage similarity (Sneath and Sokal 1973). The clusters separated below this line then represent taxa. After all efforts to use an objective method to isolate groups of leaves, the choice of percentage level is completely arbitrary. One method of choosing this level is to draw the line defining the groups at the point where there is a gap or a long branch line between nodes. This approach was not used. In this study, long branch lines do not occur at the same percentage level of similarity throughout the dendrograms, which is a problem that has been observed elsewhere (e.g. Hall 1997). In Dolph's (1976) study of living leaves of known identification, phenons were not very successful in delineating natural species. Hill (1980b) (and references cited therein) considered this approach to be invalid as well as subjective. Hill (1980a) found that clusters were easily delimited visually, but has also proposed a stopping rule for the partitioning of dendrograms (Hill 1980b). This established a quantitative criterion for the objective identification of the 'optimum' number of groups in a dendrogram. This is applicable to the mix of binary, multistate and continuous characters used in this study, and is fairly easy to calculate. However, this method was not considered suitable (see Section 4.4.3).

Dolph (1976) obtained most accurate results by visually assessing clusters of OTUs from a dendrogram in tandem with an ordination produced by principal components analysis. However, it is inappropriate to carry out principal components analysis or principle coordinates analysis using this combination of data types and the Gower Similarity Coefficient (M. Wills pers. comm.). It was considered that the best method of interpreting the dendrogram was to use it as a tool to aid in the visual identification of leaf morphotypes. Individuals of a single taxonomic group were expected to occur within a compact cluster and be isolated by a long branch line (Hall 1997). The clustering output was therefore evaluated in conjunction with the original drawings and descriptions and the morphotypes were defined.

4.4.3 Results

The dendrograms produced for these Cretaceous Antarctic angiosperm leaves are shown in Figure 4.4, Figure 4.5, and Figure 4.6. There are separate dendrograms for the Hidden Lake Formation (Figure 4.4) and the Santa Marta Formation (Figure 4.5) and a clustering analysis of the leaves from both floras together (Figure 4.6).

Figure 4.4 Hidden Lake Formation flora dendrogram.

Gower General Similarity Coefficient

Figure 4.5 Santa Marta Formation flora dendrogram

UPGMA

Gower General Similarity Coefficient
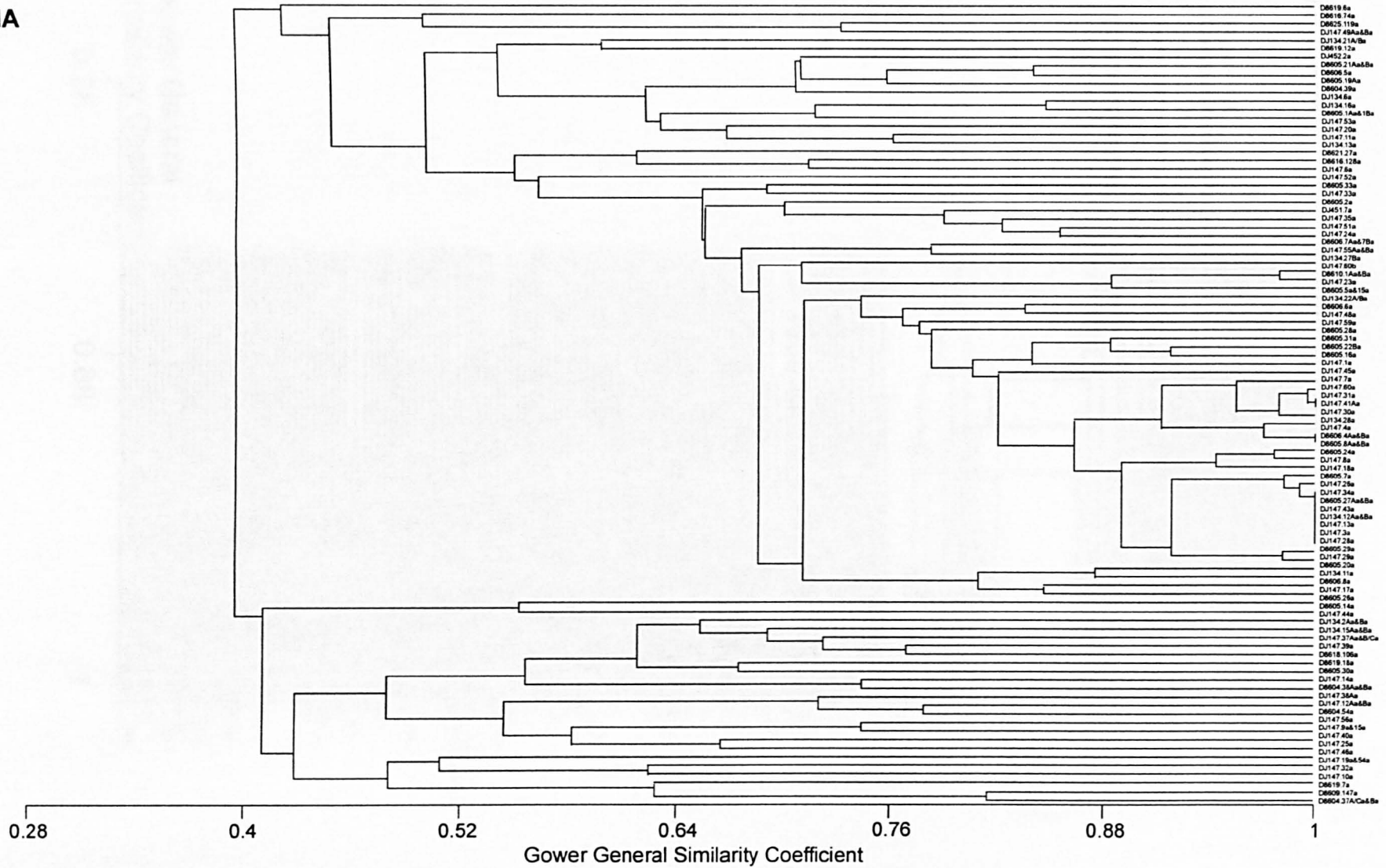
UPGMA

**Figure 4.6
Composite dendrogram
for both the Hidden Lake
Formation and Santa
Marta Formation floras.
(M = Morphotype).**
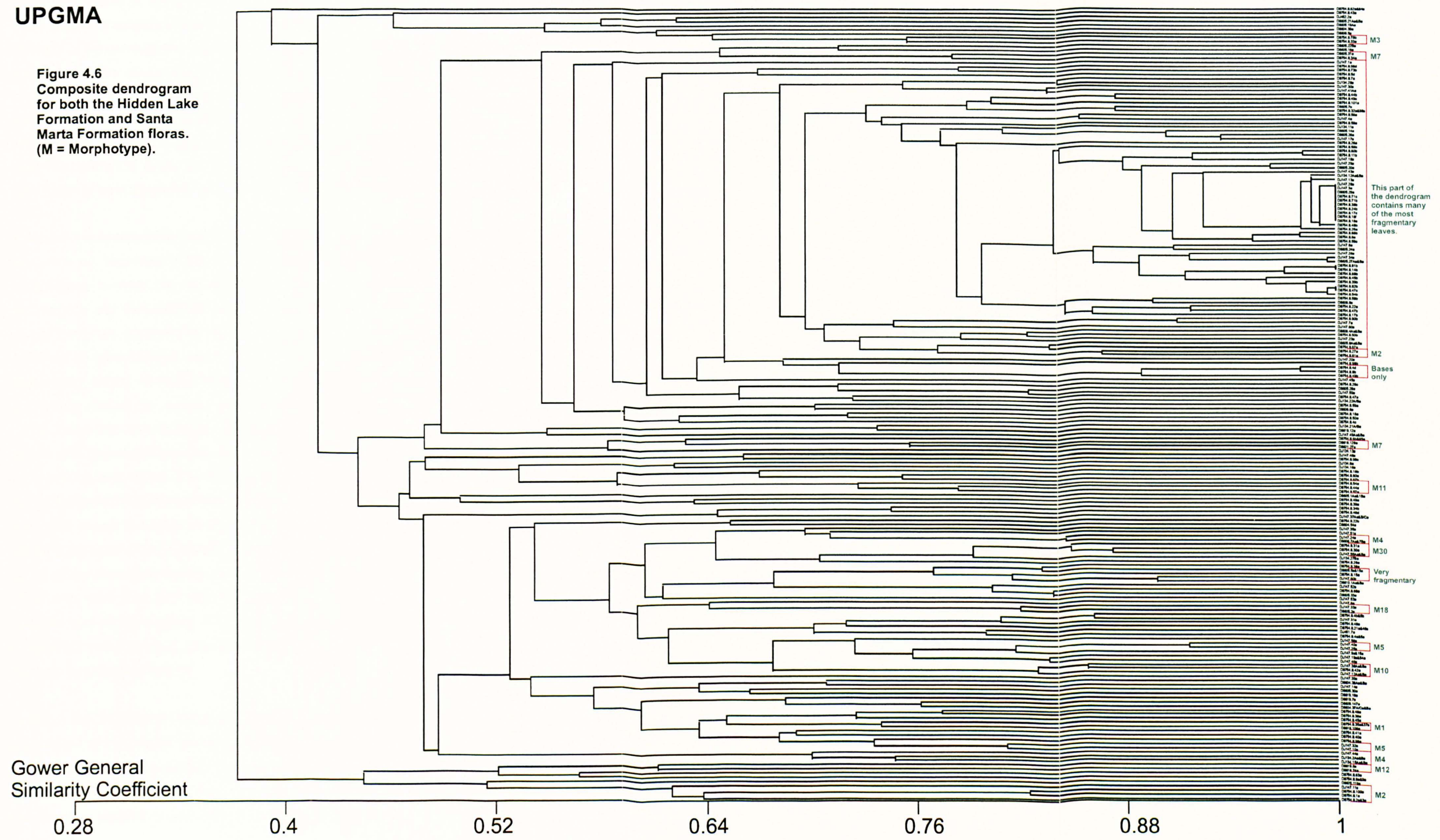
Gower General
Similarity Coefficient

0.28   0.4   0.52   0.64   0.76   0.88   1

The dendrograms clustered specimens with similar features together. Using the dendrograms along with the original data, it was possible to identify a clustering of specimens and then to confirm that this group was a separate taxon through comparison with the next cluster of specimens. Some of these clusters are marked in Figure 4.6 using the morphotype number these groups of specimens were ultimately given (Table 4.11). An example is Morphotype 2 at the base of the dendrogram. The OTUs of this cluster, with actinodromous venation and crenate margins, are very clearly different to the next closest OTU, with pinnate venation and a toothed margin. Although this clustering is based on the composite dendrogram, the dendrograms of the individual floras were also studied to ensure that groups of OTUs clustered by the composite tree were not represented as greatly dissimilar within the separate dendrograms for the Hidden Lake Formation and Santa Marta Formation floras. The dendrograms for the individual floras were found to be in agreement with the composite dendrogram for the clusters recognised.

However, it is apparent that a fairly large number of specimens were clustered together because they were too fragmentary (see Figure 4.6). These specimens could not be grouped with the morphotypes to which they belong because there was too much missing data. This was the main reason why the application of a quantitative criterion to delineate taxonomic groups (e.g. the stopping rule proposed by Hill 1980b) was considered inappropriate in this study. Dolph (1976), in his tests based on modern leaves, simulated the effect of missing data caused by the fragmentary nature of fossil material by randomly deleting variables. This was found to significantly reduce the number of correct identifications. Even without missing data, Dolph (1976) found that least confused classification resulted from a reduced sample size. The next stage in this numerical taxonomic study of Cretaceous Antarctic leaves was, therefore, to repeat the clustering analysis with the most fragmentary specimens removed. All OTUs with more than four variables missing were omitted from the analysis. The results are shown in Figure 4.7. This initial limit of only including OTUs with at least 19 of the characters preserved was selected following repeated runs of the clustering process, beginning with only the very best preserved leaves and successively adding leaves with decreasing numbers of characters present. When OTUs with more than four variables missing were included in the analysis leaves that had clustered very closely together in the earlier dendrograms, and which were considered visually to represent one taxon (e.g. members of Morphotype 2), became separated by the inclusion of the more fragmentary material.

Based on the relationships demonstrated by the dendrogram in Figure 4.7, accompanied by an assessment of the original drawings and descriptions, leaves that are the most similar can be grouped together and separated into morphotypes. For example, specimens DJ147.10a and DJ147.32a are clearly very similar and are grouped together in Morphotype 5 (Chapter 5). It was therefore possible to delineate 21 morphotypes, based on the best preserved leaves (see Figure 4.7).

Figure 4.7 Clustering of only the best preserved leaves within the Hidden Lake Formation and Santa Marta Formation floras. All OTUs have a maximum of four variables missing.
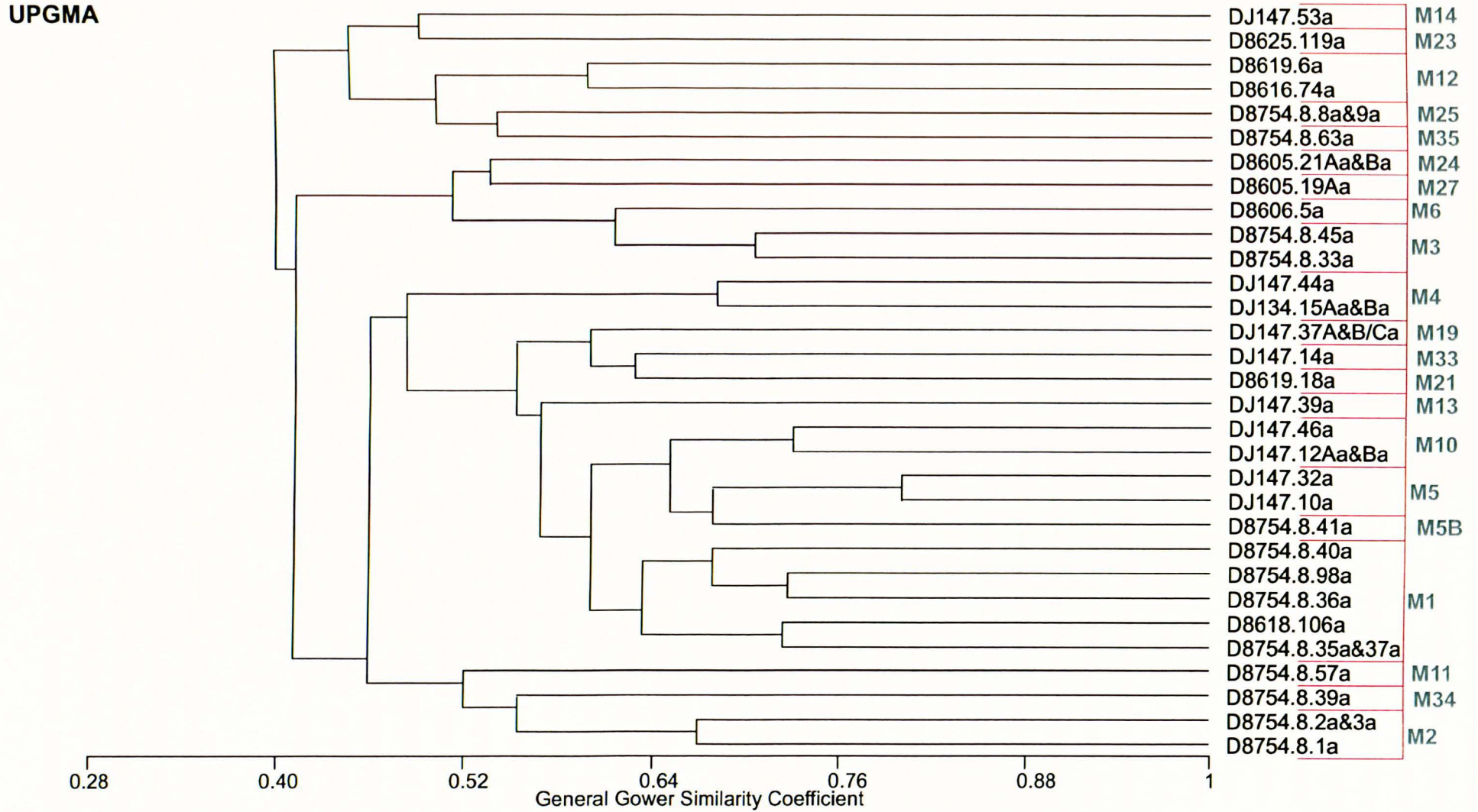
It was then attempted to assign the more fragmentary leaves (i.e. those with more than four variables missing) to these 21 morphotypes established from only the best preserved material. Taking each OTU individually, the morphotype with which a fragment showed the greatest similarity was assessed by repeating the cluster analysis using only those characters available in that fragmentary specimen. This procedure was carried out for each of the leaves, beginning with the best preserved and ending with those with the fewest characters present. For example, in the composite dendrogram of all the leaves of both floras (Figure 4.6), there is a cluster, designated M2, encompassing D8754.8.1a, D8754.8.2a&3a, D8754.8.100a and DJ147.11a. Considering only the most complete leaves (Figure 4.7), D8754.8.1a and D8754.8.2a&3a clustered together, but D8754.8.100a and DJ147.11a were too incomplete to be included. Taking DJ147.11a as an example, as for all the OTUs, a dendrogram including this specimen with the better preserved leaves was produced using only those characters present in the fragmentary leaf, DJ147.11a. Figure 4.8a is an example section of this dendrogram, illustrating that when the number of characters is reduced to include only those present in the fragmentary material, specimens such as DJ147.11a do cluster with leaves with the most similar architecture, Morphotype 2 (Chapter 5). Similar results were also obtained for D8754.8.100a (Figure 4.8b). Using this approach, it was possible to assign even very fragmentary material to morphotypes. For example, in the original dendrogram (Figure 4.6), D8754.8.58a was simply clustered within the large heterogeneous group of fragmentary specimens. This leaf fragment has only ten of the variables used in the analysis, features of the leaf base, margin, and secondary and tertiary veins. Figure 4.8c is a part of the dendrogram created using only these characters and it is then clear that D8754.8.58a clusters with the leaves of Morphotype 2.

This process was carried out for all the fragmentary specimens and in this way, many were assigned to one of the 21 morphotypes already established. However, using this procedure, it was also clear when one of these less well preserved leaves did not fit into any of the morphotypes based on almost whole leaves. For example, D8754.8.43a has only five variables that cannot be scored. Figure 4.8d shows part of the dendrogram resulting from a clustering analysis based on the remaining 18 characters. D8754.8.43a clusters with a group containing three different morphotypes (M6, M24 and M27), and these are all more similar to each other than D8754.8.43a is to any one of them. The leaf D8754.8.43a is therefore established as a separate morphotype (M36). This new morphotype was then included in the subsequent analyses of the more fragmentary material. Thus, each OTU was either added to an existing morphotype or used to create a new morphotype. This resulted in the definition of a total of 41 morphotypes (Figure 4.9, Table 4.11).

Using this approach, the best preserved material has the greatest influence over the resulting classification, but it is also possible to include very fragmentary material. Combined with knowledge of the leaf specimens from the original drawings and descriptions, this multivariate statistical approach was a useful tool in the grouping of these Late Cretaceous Antarctic angiosperm leaves into morphotypes. Only a relatively small number of residual scrappy

fragments (less than 20% of the specimens) containing very few diagnostic features could not be grouped into morphotypes.

A total of 41 morphotypes were established and the specimens assigned to each morphotype are presented in Table 4.11. Of these 41 morphotypes, 30 are present within the Hidden Lake Formation flora and 31 are present within the Santa Marta Formation flora. Twenty of the morphotypes are common to both floras, while the remaining 21 are specific to one flora or the other. Figure 4.10 and Figure 4.11 are compilations to show a typical example of each morphotype.

In Figure 4.9, groups of morphotypes appear to be clustered together. In the central part of the dendrogram, the morphotypes (16, 17, 30, 29, 8, 9, 15, 14, 26, 27, 36, 18, 24, 6 and 3) appear to show a range of characteristics and there is no one feature that clearly unites them. However, Morphotypes 32, 31, 37, 40, 38, 7, 12, 35 and 25 are separated from the rest of the morphotypes. None of the leaves within these nine morphotypes have entire margins present. All of these morphotypes possess leaves with toothed, crenate, erose or lobed margins. Also within this group, Morphotypes 32, 31 and 37 cluster together and differ from the remaining six in that they do not possess pinnate venation but rather actinodromous or palinactinodromous venation. Morphotypes 39, 20, 19, 22, 21, 13, 1, 28, 33, 10, 5B, 5 and 4 form a group within which all of the leaves have pinnate venation. The observed venation pattern in all these leaves is either pinnate camptodromous brochidodromous, eucamptodromous or semicraspedodromous. The average angle of origin of the basal secondary veins from the midvein is also narrow to moderately acute in these 13 morphotypes. At the bottom of the dendrogram, Morphotypes 23, 11, 34 and 2 are clustered together. All of these four morphotypes contain leaves with an ovate form, none possess a petiole or outer secondary veins and the average angle of tertiary vein origin on the admedial side of the secondaries is approximately right-angled in all of these morphotypes.

4.4.3.1 Summary of the features of each morphotype (Tables 4.12-4.14)

Following the approach adopted by Hill (1982), the range of characteristics used in the clustering analysis for each morphotype is given in Tables 4.12, Table 4.13 and Table 4.14. These form the basis of this study and additional information is presented in a description of each morphotype in Chapter 5.

At the head of each column the numbers in brackets refer to the character numbers used in the analysis (see Table 4.10).

M – Morphotype

NS – Number of specimens

symm. – symmetrical   asymm. – asymmetrical

A – acute   R – right-angled   O – obtuse
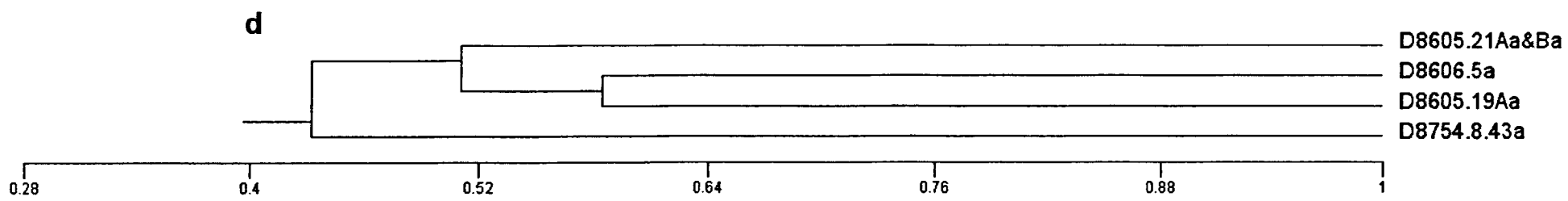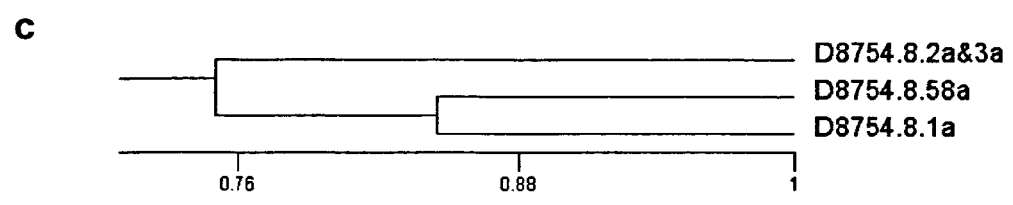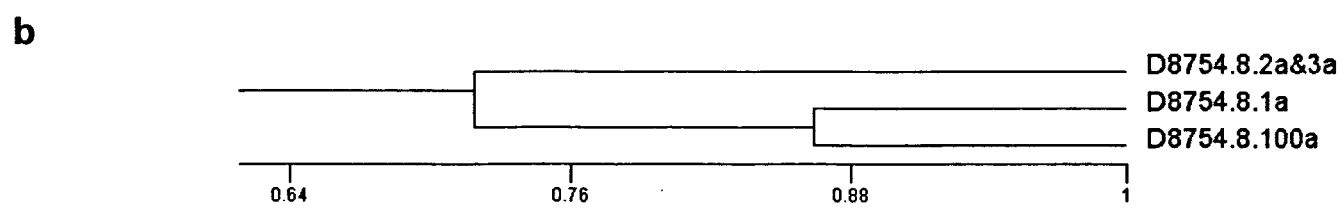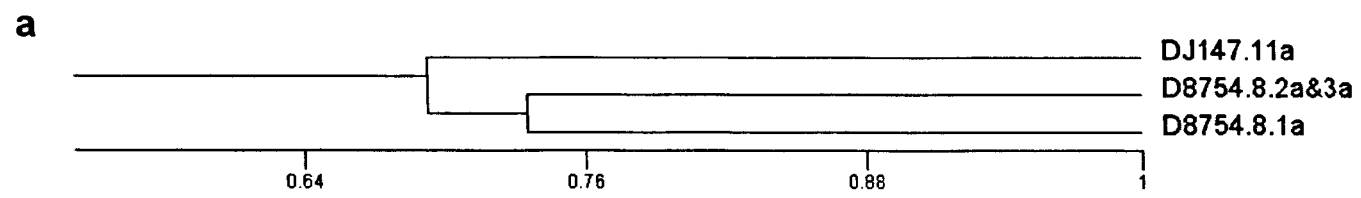
Figure 4.8 Example sections of dendrograms produced
using a subset of the original variables.

Figure 4.9 Clustering of the 41 morphotypes defined for these Late Cretaceous Antarctic leaves. (M = Morphotype).
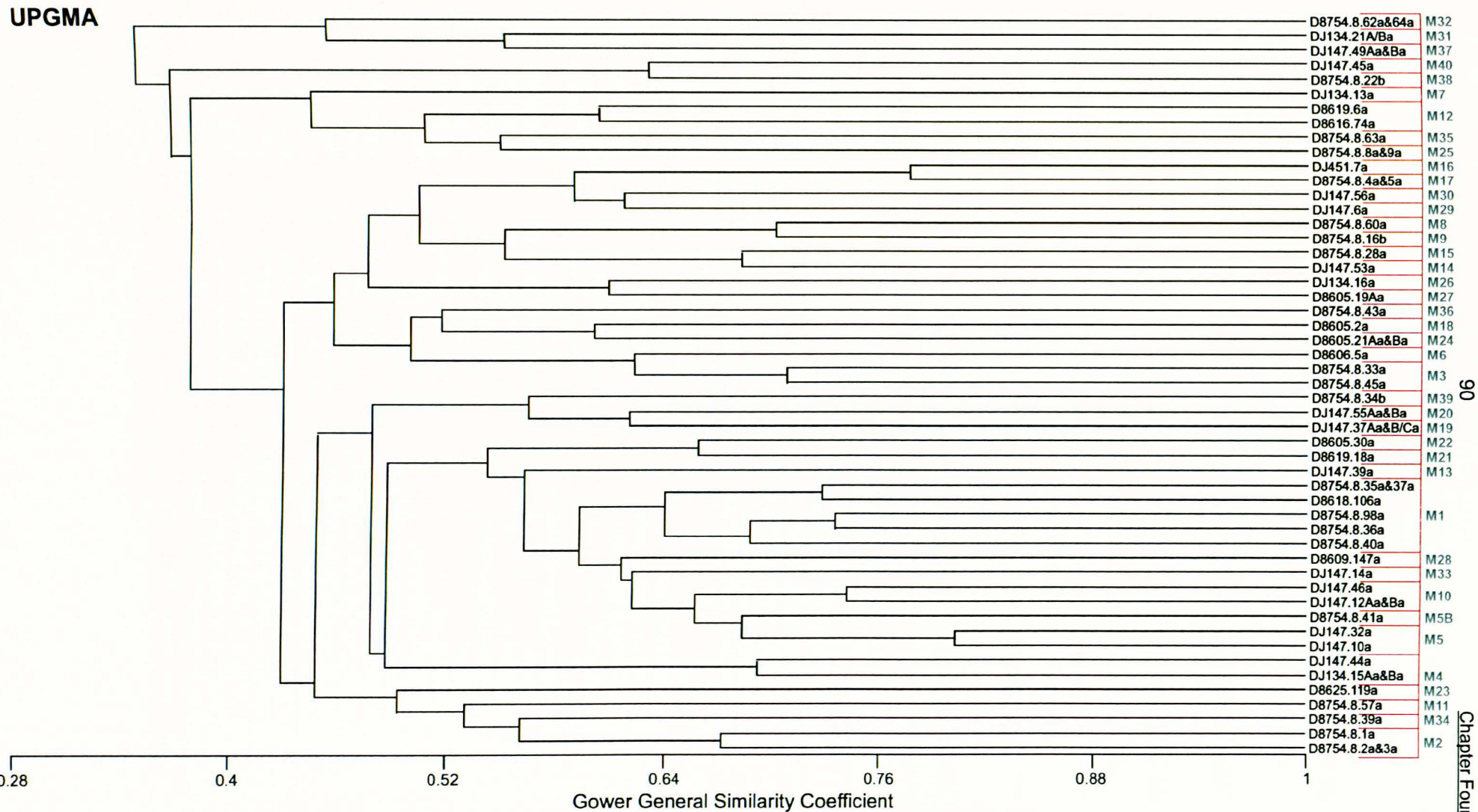
M	Hidden Lake Formation flora	Santa Marta Formation flora
1	D8754.8.35a&37a, D8754.8.36a, D8754.8.40a, D8754.8.98a, D8754.8.98c, D8754.8.49a, D8754.8.16a, D8754.8.67a, D8754.8.22a	D8618.106a, DJ147.9a&15a, DJ147.48a, DJ147.60b, DJ147.31a, DJ147.60a, D8605.8Aa&Ba, DJ147.26a
2	D8754.8.1a, D8754.8.2a&3a, D8754.8.100a, D8754.8.61a, D8754.8.27a, D8754.8.58a	DJ147.11a, D8619.12a, DJ147.23a, DJ147.20a
3	D8754.8.33a, D8754.8.45a, D8754.8.46a, D8754.8.68a, D8754.8.76b, D8754.8.5d, D8754.8.59c	D8619.7a, D8605.5a&15a, D8606.4Aa&Ba
4	D8754.8.17b, D8754.8.4d	DJ134.15Aa&Ba, DJ147.44a, D8606.7Aa&Ba, DJ134.2Aa&Ba, DJ147.24a, DJ147.41Aa, DJ134.28a
5	D8754.8.7a	DJ147.10a, DJ147.32a, DJ147.25a, DJ147.40a
5B	D8754.8.41a	D8610.1Aa&Ba, D8605.26a
6	D8754.8.50a, D8754.8.98d	D8606.5a, DJ452.2, DJ147.51a, DJ147.59a, D8606.6a
7	D8754.8.34a	DJ134.13a, DJ147.35a, D8621.27a, DJ134.22A/Ba, D8605.31a, D8616.128a, D8605.7a
8	D8754.8.60a, D8754.8.8b, D8754.8.54b, D8754.8.60b	D8605.27Aa&Ba, DJ147.4a, DJ147.30a, DJ147.34a
9	D8754.8.16b	
10	D8754.8.42a, D8754.8.4b&5b, D8754.8.15a	DJ147.12Aa&Ba, DJ147.46a, DJ147.19a&54a, DJ147.38Aa
11	D8754.8.57a, D8754.8.54a, D8754.8.44a	D8605.33a, DJ147.52a, DJ134.6a
12	D8754.8.47a, D8754.8.32a&98e, D8754.8.101a	D8616.74a, D8619.6a, D8606.8a
13	D8754.8.21a&46e	DJ147.39a, D8604.37A/Ca&Ba, D8604.54a, DJ147.1a
14	D8754.8.67b, D8754.8.4c, D8754.8.38a	DJ147.53a
15	D8754.8.28a	
16		DJ451.7a
17	D8754.8.4a&5a	
18	D8754.8.26c	D8605.2a, DJ147.33a, DJ147.7a
19		DJ147.37A&B/Ca, DJ134.27Ba, D8605.16a
20	D8754.8.30a, D8754.8.31a	DJ147.55Aa&Ba
21	D8754.8.98b, D8754.8.47b	D8619.18a
22		D8605. 30a
23	D8754.8.49b	D8625.119a, DJ134.11a
24		D8605.21Aa&Ba, D8604.39a, (D8605.22Ba)
25	D8754.8.8a&9a, D8754.8.6b&65a	
26		DJ134.16a, D8605.1Aa&Ba
27		D8605.19Aa, D8605.28a
28	D8754.8.48a	D8609.147a
29		DJ147.6a, D8604.38Aa&Ba
30		DJ147.56a, D8605.24a
31	D8754.8.73b	DJ134.21A/Ba
32	D8754.8.62a&64a	
33		DJ147.14a, DJ147.17a
34	D8754.8.39a	
35	D8754.8.63a	
36	D8754.8.43a	
37		D&147.49Aa&Ba
38	D8754.8.22b	
39	D8754.8.34b	
40		DJ147.45a

Table 4.11 Specimens of the Hidden Lake Formation and Santa Marta Formation floras included within each of the 41 morphotypes defined using multivariate statistical analysis. (M = Morphotype).
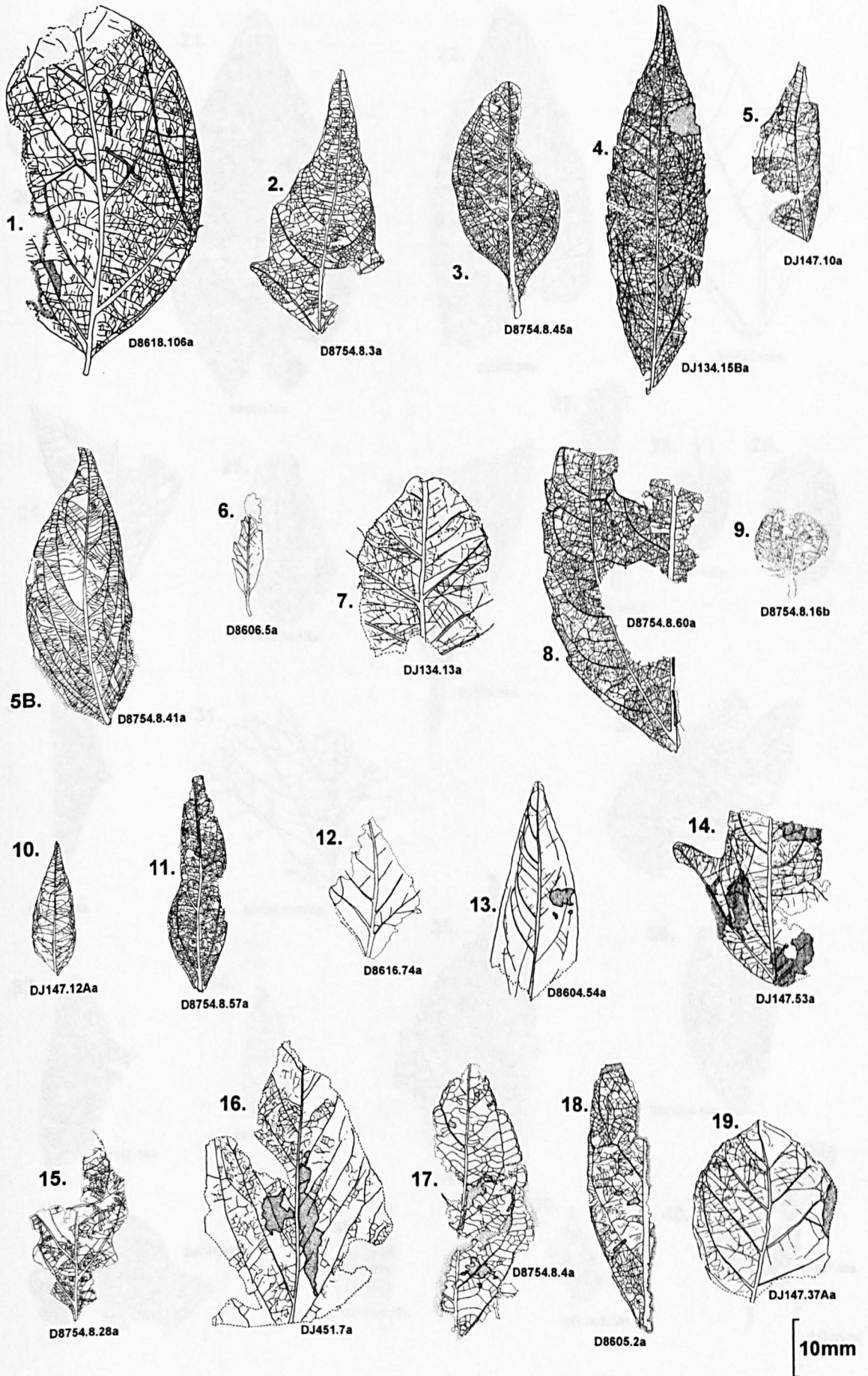
Figure 4.10 A typical leaf to illustrate each of the Cretaceous Antarctic
angiosperm leaf Morphotypes 1-19.
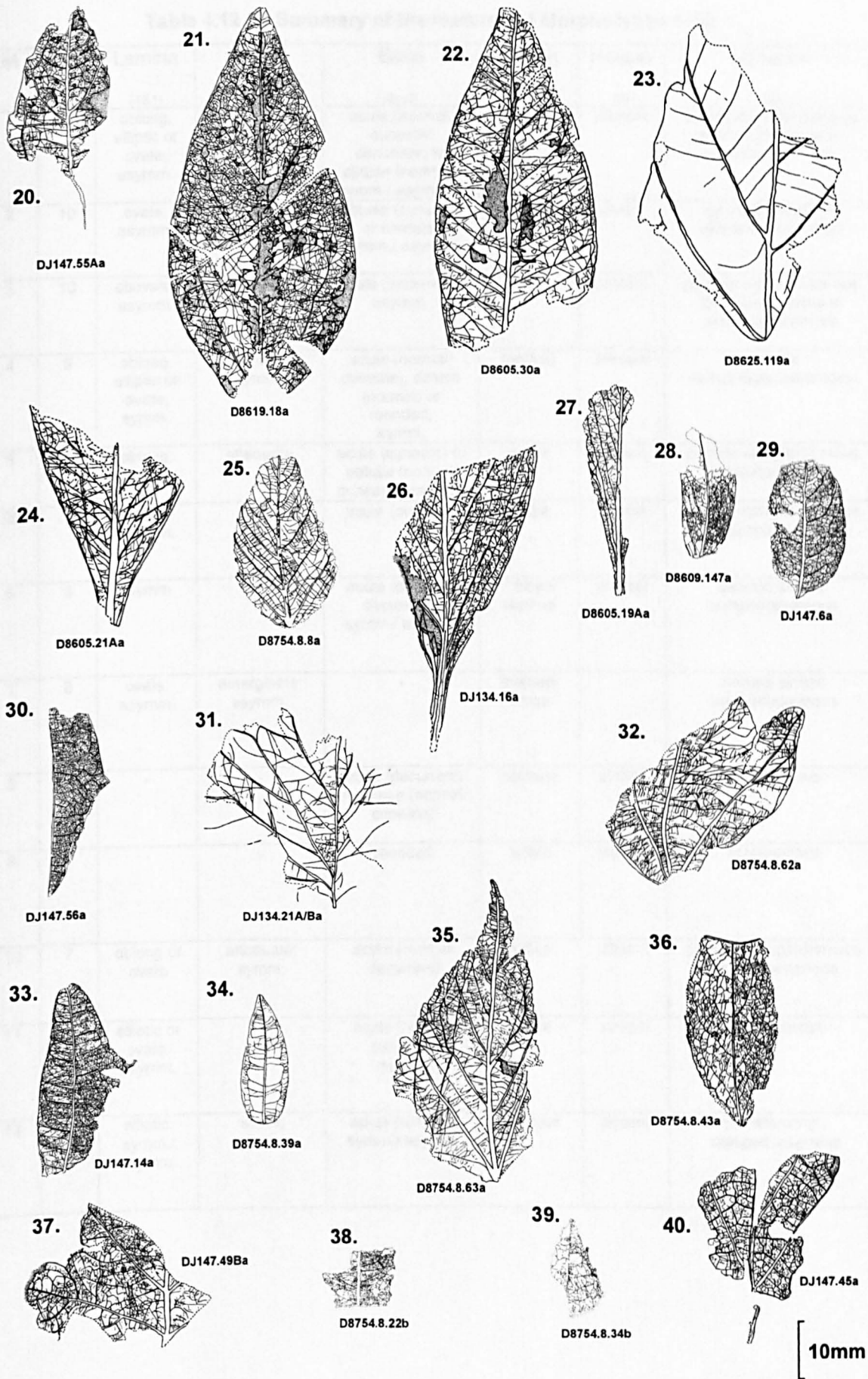
Figure 4.11 A typical leaf to illustrate each of the Cretaceous Antarctic angiosperm leaf Morphotypes 20-40.

Table 4.12 (a) Summary of the features of Morphotypes 1-12.

M	NS	Lamina (4&1)	Apex (5&3)	Base (6&2)	Margin (7)	Petiole (8)	Venation (9)
1	17	oblong, elliptic or ovate; asymm.	acute; symm./ asymm.	acute (normal, cuneate/ decurrent) to obtuse (normal); symm./ asymm.	entire	present	pinnate camptodromous brochidodromous to eucamptodromous
2	10	ovate; asymm.	attenuate; symm.	obtuse (cuneate) or cordate; symm./ asymm.	crenate	absent	actinodromous (or palinactinodromous)
3	10	obovate; asymm.	acute	acute (decurrent); asymm.	entire	present	pinnate camptodromous brochidodromous to eucamptodromous
4	9	oblong, elliptic or ovate; symm.	attenuate; symm.	acute (normal/ cuneate), obtuse (normal) or rounded; symm.	toothed	present	pinnate semicraspedodromous
5	5	oblong; asymm.	attenuate	acute (cuneate) or obtuse (normal/ cuneate); asymm.	entire	absent	pinnate camptodromous brochidodromous
5B	3	ovate; asymm.	-	acute (cuneate)	entire	absent	pinnate camptodromous eucamptodromous
6	8	asymm.	-	acute (cuneate/ decurrent); symm./ asymm.	? lobed/ toothed	present	pinnate simple craspedodromous
7	8	ovate; asymm.	emarginate; asymm.	-	toothed/ erose	-	pinnate simple craspedodromous
8	8	-	-	acute (decurrent) or obtuse (normal/ cuneate)	toothed	absent	acrodromous
9	1	-	-	rounded	entire	present	acrodromous
10	7	oblong or ovate	attenuate; symm.	acute (normal/ decurrent)	entire	absent	pinnate camptodromous brochidodromous
11	6	elliptic or ovate; asymm.	-	acute (normal/ cuneate); symm.	entire	absent	acrodromous
12	6	elliptic; symm./ asymm.	acute; symm.	acute (normal); symm./ asymm.	toothed	absent	pinnate simple craspedodromous

Table 4.12 (b) Summary of the features of Morphotypes 1-12.

M.	1° vein size (10)	1° vein course (11)	average 2° angle (12)	basal 2° angle (13)	2° angle variation (14 & 15)	2° course (16 & 17)
1	moderate to stout	straight to curved	moderate acute 43-78° avg. 62.5° s.d. 9.95°	moderate acute 40-79° avg. 58.1° s.d. 13.6°	nearly uniform to irregular; symm./ asymm.	curved; branched/ unbranched
2	weak to stout	straight to curved	wide acute 44-89° avg. 69.5° s.d. 13.2°	moderate acute 44-75° avg. 58.4° s.d. 12°	upper 2°s more obtuse, lowest pair more acute than all others, or irregular; symm./ asymm.	curved; unbranched
3	stout to massive	straight	moderate acute 38-69° avg. 52.2° s.d. 7.96°	narrow acute 12-62° avg. 33.3° s.d. 16.3°	lowest pair more acute than all others or irregular; symm./ asymm.	curved; branched/ unbranched
4	stout to massive	straight to curved	moderate acute 50-66° avg. 58.1° s.d. 5.05°	moderate acute 37-73° avg. 50.2° s.d. 16.2°	irregular; symm./ asymm.	curved; branched
5	stout	curved	wide acute 52-77° avg. 69.6° s.d. 9°	moderate acute 50-56° avg. 53° s.d. 3°	irregular; symm./ asymm.	curved; branched
5B	stout	straight to curved	narrow acute 38-48° avg. 44.3° s.d. 4.5°	narrow acute 40°	irregular; symm./ asymm.	curved; branched/ unbranched
6	massive	straight	narrow acute 11-74° avg. 43.1° s.d. 20.2°	narrow acute 8-66° avg. 41° s.d. 18.1°	nearly uniform to irregular; symm./ asymm.	recurved, curved or sinuous; branched/ unbranched
7	weak to stout	straight	moderate acute 27-68° avg. 49.1° s.d. 14.9°	narrow acute 31°	nearly uniform to irregular; symm.	recurved or sinuous; branched/ unbranched
8	weak to stout	straight	-	narrow acute 38-40° avg. 39° s.d. 1.25°	-	curved; branched/ unbranched
9	stout	straight	-	wide acute 66°	asymm.	curved; unbranched
10	stout	straight to curved	wide acute 61-87° avg. 72.4° s.d. 8.97°	moderate acute 36-98° avg. 64.6° s.d. 22.4°	upper 2°s more obtuse, lowest pair more acute than all others, or irregular; symm./ asymm.	curved; branched
11	stout to massive	straight to curved	moderate acute 37-63° avg. 50.6° s.d. 8.55°	narrow acute 26-50° avg. 36.1° s.d. 7.74°	nearly uniform or lowest pair more acute than all others; symm./ asymm.	curved; unbranched
12	stout	straight to curved	moderate acute 44-65° avg. 50.6° s.d. 7.71°	narrow acute 30-37° avg. 33.5° s.d. 3.5°	upper 2°s more obtuse or acute, or lowest pair more acute than all others; asymm.	recurved; branched/ unbranched

Table 4.12 (c) Summary of the features of Morphotypes 1-12.

M.	Outer 2° veins (18)	Intersecondary veins (19)	Intramarginal vein (20)	Average admedial 3° angle (21)	Average exmedial 3° angle (22)	Average midvein 3° angle (23)
1	absent	present	absent	R 66-110° avg. 88.5° s.d. 10.8°	A 42-86° avg. 71.6° s.d. 11.7°	R 61-101° avg. 80.5° s.d. 10.1°
2	absent	absent	absent	R 80-96° avg. 87.1° s.d. 5.44°	R 66-111° avg. 88.2° s.d. 12.9°	R 82-98° avg. 90.4° s.d. 5.55°
3	absent	present	absent	R 82-106° avg. 92.2° s.d. 7.34°	A 38-95° avg. 71.2° s.d. 16.8°	A 63-89° avg. 77° s.d. 8.31°
4	absent	present	absent	R 71-92° avg. 82.9° s.d. 7.49°	A 58-90° avg. 71.9° s.d. 9.57°	R 67-94° avg. 80.8° s.d. 9.62°
5	absent	present	absent	R 77-92° avg. 84.3° s.d. 5.58°	R 71-87° avg. 80.2° s.d. 5.51°	R 80-97° avg. 89.3° s.d. 6.06°
5B	absent	present	absent	R 81-90° avg. 85° s.d. 3.74°	R 89-94° avg. 91.3° s.d. 2.05°	R 80-83° avg. 81.6° s.d. 1.21°
6	absent	present	absent	A 59-105° avg. 74.3° s.d. 14.6°	R 51-111° avg. 84.9° s.d. 20.6°	R 56-141° avg. 93.3° s.d. 35.5°
7	present	present	absent	R 79-113° avg. 97.7° s.d. 12.8°	A 48-94° avg. 74.4° s.d. 16.3°	R 70-127° avg. 92.2° s.d. 21.5°
8	absent	absent	absent	R 73-90° avg. 82.2° s.d. 5.54°	A 72-82° avg. 75.5° s.d. 3.68°	A 77-80° avg. 78.5° s.d. 1.5°
9	absent	absent	absent	R 90°	R 82°	R 89°
10	absent	present	absent	R 75-97° avg. 87.1° s.d. 7.07°	R 67-92° avg. 84.7° s.d. 7.95°	R 69-89° avg. 81.2° s.d. 6.5°
11	absent	present	absent	R 87-97° avg. 90.7° s.d. 3.17°	A 69-86° avg. 74.6° s.d. 5.46°	R 70-124° avg. 81.6° s.d. 19.2°
12	present	absent	absent	A 62-79° avg. 72.2° s.d. 6.11°	A 53-96° avg. 78.8° s.d. 14.8°	A 76-84° avg. 79.1° s.d. 3.75°

Table 4.13 (a) Summary of the features of Morphotypes 13-28.

M	NS	Lamina (4&1)	Apex (5&3)	Base (6&2)	Margin (7)	Petiole (8)	Venation (9)
13	5	oblong or ovate; asymm.	attenuate; symm./ asymm.	acute (normal)	entire/ lobed	present	pinnate camptodromous brochidodromous
14	4	ovate; asymm.	-	obtuse (normal)	entire/ lobed	absent	actinodromous (to acrodromous)
15	1	-	-	acute (decurrent)	crenate	absent	pinnate mixed craspedodromous
16	1	-	-	-	-	-	pinnate camptodromous eucamptodromous
17	1	-	symm.	-	-	-	actinodromous
18	4	oblong	-	acute (cuneate)	entire	absent	pinnate camptodromous brochidodromous
19	3	elliptic; asymm.	obtuse; asymm.	-	crenate/ erose	absent	pinnate camptodromous brochidodromous
20	3	-	acute	-	crenate	-	pinnate semicraspedodromous
21	3	ovate; asymm.	acute; asymm.	asymm.	entire	-	pinnate camptodromous brochidodromous
22	1	asymm.	acute	-	entire	-	pinnate camptodromous brochidodromous
23	3	ovate; asymm.	-	obtuse (normal); asymm.	toothed/ crenate	absent	pinnate simple craspedodromous
24	3	asymm.	-	acute (decurrent); symm./ asymm.	entire	absent	pinnate camptodromous brochidodromous
25	2	ovate; asymm.	acute; asymm.	obtuse (normal); asymm.	toothed/ erose	absent	pinnate simple craspedodromous
26	2	oblong	-	acute (cuneate); symm.	entire	present	pinnate camptodromous brochidodromous to eucamptodromous
27	2	-	-	acute (decurrent); symm.	erose	present	pinnate simple craspedodromous
28	2	oblong	-	-	entire	-	pinnate camptodromous brochidodromous

Table 4.13 (b) Summary of the features of Morphotypes 13-28.

M.	1° vein size (10)	1° vein course (11)	average 2° angle (12)	basal 2° angle (13)	2° angle variation (14 & 15)	2° course (16 & 17)
13	stout to massive	straight to curved	moderate acute 33-79° avg. 50.8° s.d. 15.3°	moderate acute 47°	nearly uniform to irregular; symm./ asymm.	curved; branched
14	weak to stout	straight	moderate acute 53-63° avg. 58° s.d. 4.08°	narrow acute 20-47° avg. 35.4° s.d. 11.2°	upper 2°s more obtuse; symm./ asymm.	recurved or curved; branched/ unbranched
15	stout	straight	moderate acute 56°	narrow acute 38°	upper 2°s more obtuse; asymm.	curved; branched
16	moderate	straight	narrow acute 35°	narrow acute 35°	upper 2°s more obtuse; symm.	curved; branched
17	moderate	straight	moderate acute 58°	-	upper 2°s more acute; symm.	curved; branched
18	massive	straight	moderate acute 44-78° avg. 60° s.d. 14.7°	narrow acute 34-43° avg. 38.5° s.d. 4.5°	nearly uniform or lowest pair more acute than all others	curved; branched
19	weak to stout	straight to curved	moderate acute 45-63° avg. 52° s.d. 7.87°	moderate acute 46°	irregular; asymm.	curved; branched
20	stout	straight to curved	wide acute 68-76° avg. 72.3° s.d. 3.3°	-	irregular; asymm.	curved; branched
21	moderate	straight	narrow acute 40-49° avg. 43.3° s.d. 4.03°	-	irregular; symm./ asymm.	curved; branched
22	stout	straight	moderate acute 53°	-	irregular; symm.	curved; unbranched
23	moderate	straight	moderate acute 41-50° avg. 45.5° s.d. 4.5°	moderate acute 56-58° avg. 57° s.d. 1°	nearly uniform or upper 2°s more acute; asymm.	curved; unbranched
24	stout to massive	straight	narrow acute 26-39° avg. 32.5° s.d. 6.5°	narrow acute 30°	irregular; symm.	recurved or sinuous; branched
25	stout	curved	moderate acute 53-61° avg. 57° s.d. 4°	moderate acute 51°	irregular; symm./ asymm.	recurved or curved; unbranched
26	stout	curved	narrow acute 35-40° avg. 37.5° s.d. 2.5°	narrow acute 12°	upper 2°s more obtuse; symm.	straight or recurved; branched/ unbranched
27	massive	straight	narrow acute 24-51° avg. 37.5° s.d. 13.5°	narrow acute 16°	upper 2°s more obtuse; symm.	straight or recurved; branched/ unbranched
28	stout	curved	moderate acute 53-54° avg. 53.5° s.d. 0.5°	-	lowest pair more acute than all others or irregular; symm./ asymm.	curved or sinuous; branched

Table 4.13 (c) Summary of the features of Morphotypes 13-28.

M.	Outer 2° veins (18)	Intersecondary veins (19)	Intramarginal vein (20)	Average admedial 3° angle (21)	Average exmedial 3° angle (22)	Average midvein 3° angle (23)
13	absent	present	absent	R 67-91° avg. 81.2° s.d. 9.09°	R 83-110° avg. 96.7° s.d. 11.9°	A 59-75° avg. 66.8° s.d. 7.27°
14	absent	present	absent	R 77-97° avg. 85.8° s.d. 8.25°	A 69-79° avg. 73.7° s.d. 3.74°	R 54-104° avg. 81.1° s.d. 20.3°
15	absent	present	absent	O 101°	A 61°	R 86°
16	absent	present	absent	A 76°	R 94°	O 100°
17	absent	present	-	R 88°	A 72°	A 72°
18	absent	absent	absent	R 94-96° avg. 94.7° s.d. 0.94°	R 77-90° avg. 82° s.d. 5.72°	R 88-90° avg. 89° s.d. 1°
19	present	present	absent	R 83-94° avg. 88° s.d. 4.55°	A 68-78° avg. 74.7° s.d. 4.71°	R 86-101° avg. 93° s.d. 6.16°
20	present	present	absent	R 83-96° avg. 89° s.d. 5.4°	A 69-84° avg. 75.8° s.d. 6.26°	R 72-105° avg. 84° s.d. 14.7°
21	absent	absent	absent	R 76-97° avg. 89.3° s.d. 9.24°	R 74-89° avg. 82.2° s.d. 6.11°	R 90-95° avg. 92.5° s.d. 2.5°
22	absent	absent	present	R 94°	R 82°	O 102°
23	absent	absent	absent	R 77-94° avg. 85.9° s.d. 6.96°	A 59-87° avg. 69.8° s.d. 12.3°	O 87-111° avg. 102° s.d. 10.6°
24	present	absent	present	R 80°	A 47-77° avg. 62° s.d. 15°	R 92°
25	absent	present	absent	R 93-94° avg. 93.2° s.d. 0.53°	R 76-98° avg. 86.9° s.d. 11.1°	O 103-119° avg. 111.2° s.d. 7.78°
26	absent	present	present	R 92-95° avg. 93.5° s.d. 1.5°	A 64-83° avg. 73.5° s.d. 9.5°	R 94°
27	absent	present	absent	R 85-93° avg. 89° s.d. 4°	A 43-77° avg. 60° s.d. 17°	R 98°
28	absent	present	absent	A 78° avg. 77.9° s.d. 0.15°	R 95-102° avg. 98.7° s.d. 3.65°	A 76-78° avg. 76.9° s.d. 0.9°

Table 4.14 (a) Summary of the features of Morphotypes 29-40.

M	NS	Lamina (4&1)	Apex (5&3)	Base (6&2)	Margin (7)	Petiole (8)	Venation (9)
29	2	asymm.	obtuse; asymm.	obtuse (normal)	entire	absent	pinnate camptodromous reticulodromous
30	2	-	-	acute (normal)	entire	absent	pinnate camptodromous brochidodromous
31	2	asymm.	-	obtuse (cuneate); asymm.	-	present	palinactinodromous
32	1	asymm.	-	obtuse (normal); asymm.	lobed	absent	palinactinodromous
33	2	oblong; asymm.	acute; asymm.	-	entire	-	pinnate camptodromous brochidodromous
34	1	ovate; symm.	acuminate; symm.	rounded; symm.	entire	absent	pinnate camptodromous brochidodromous
35	1	ovate; asymm.	acuminate	asymm.	erose	absent	pinnate camptodromous eucamptodromous
36	1	-	-	acute (decurrent)	toothed	absent	pinnate camptodromous brochidodromous
37	1	ovate	-	hastate	lobed	present	actinodromous
38	1	-	-	-	crenate	-	pinnate camptodromous brochidodromous
39	1	asymm.	-	-	crenate	-	-
40	1	-	-	lobate	crenate	absent	-

Table 4.14 (b) Summary of the features of Morphotypes 29-40.

M.	1° vein size (10)	1° vein course (11)	average 2° angle (12)	basal 2° angle (13)	2° angle variation (14 & 15)	2° course (16 & 17)
29	stout to massive	straight	wide acute 69-73° avg. 71° s.d. 2°	approx. right-angled 94°	irregular; symm.	curved; branched
30	moderate	curved	approx. right-angled 86°	wide acute 74°	lowest pair more acute than all others	curved; branched
31	weak	straight	narrow acute 33-43° avg. 38° s.d. 5°	narrow acute 43°	asymm.	-
32	moderate	curved	wide acute 69°	wide acute 69°	-	-
33	stout	curved	approx. right-angled 82-85° avg. 84° s.d. 1.5°	-	nearly uniform; symm./asymm.	curved; branched/ unbranched
34	stout	curved	approx. right-angled 84°	wide acute 69°	irregular; asymm.	curved; unbranched
35	stout	curved	moderate acute 46°	narrow acute 23°	lowest pair more acute than all others; asymm.	recurved
36	moderate	straight	moderate acute 49°	narrow acute 18°	lowest pair more acute than all others; asymm.	sinuous; branched
37	weak	straight	moderate acute 48°	moderate acute 48°	asymm.	straight; unbranched
38	massive	-	wide acute 71°	-	nearly uniform; symm.	curved; unbranched
39	moderate	curved	approx. right-angled 88°	-	irregular; asymm.	sinuous; branched
40	massive	-	-	moderate acute 46°	-	straight; unbranched

Table 4.14 (c) Summary of the features of Morphotypes 29-40.

M.	Outer 2° veins (18)	Intersecondary veins (19)	Intramarginal vein (20)	Average admedial 3° angle (21)	Average exmedial 3° angle (22)	Average midvein 3° angle (23)
29	absent	present	absent	R 87-92° avg. 89.5° s.d. 2.5°	A 72-79° avg. 75.5° s.d. 3.5°	A 75-84° avg. 79.5° s.d. 4.5°
30	absent	present	absent	R 83-88° avg. 85.5° s.d. 2.5°	R 96-99° avg. 97.5° s.d. 1.5°	R 85°
31	absent	absent	absent	R 97-102° avg. 99.5° s.d. 2.5°	A 62-64° avg. 63.2° s.d. 1.15°	O 112°
32	absent	absent	absent	A 58°	A 49°	-
33	absent	present	absent	R 89-95° avg. 92° s.d. 3°	A 68-79° avg. 74° s.d. 5.5°	R 88-89° avg. 89° s.d. 0.5°
34	absent	-	absent	R 85°	A 52°	-
35	absent	present	absent	R 82°	R 83°	R 81°
36	absent	absent	absent	A 74°	O 104°	A 72°
37	absent	absent	absent	R 85°	A 67°	A 79°
38	absent	absent	absent	R 97°	A 68°	R 97°
39	absent	-	absent	R 91°	R 87°	R 96°
40	absent	absent	absent	R 85°	R 98°	R 86°

4.4.4 Summary

This chapter illustrates the attempts made to group these Cretaceous Antarctic angiosperm leaves into morphotypes. The first attempt was based on simple visual inspection of the leaves, but this was not useful because it was difficult to assess all the features of these leaves showing varying degrees of preservation. The second approach involved attempting to group all the leaves based on one character, venation type. This approach was not successful because many of the leaves were too poorly preserved for the venation type to be confidently defined. In fact, due to the fragmentary nature of the leaf material, there is not one feature that is present and can be compared for all of the leaves. For this reason, it was decided to attempt a multivariate statistical clustering of the leaves.

Due to the statistical software available, first attempts at statistical clustering of the leaves involved converting all of the observed characters into binary data. This was suitable for many of the characters, but not all. The method of clustering the leaves that was eventually used was a statistical approach using a combination of binary, multistate and continuous variables. The Gower General Similarity Coefficient was used to quantify the similarity between all of the leaves and a dendrogram was produced. Dendrograms based on all the variables and subsets of the variables were then used, along with the original drawings and descriptions, to delineate groups of leaves or morphotypes. Even very fragmentary material could be included within the analysis. In total, 69% of the Hidden Lake Formation leaves and 89% of the Santa Marta Formation leaves were assigned to 41 morphotypes.

The morphotypes are based on a clustering of similar features. Although they were statistically produced, they are considered no different to fossil taxa defined by other means. These morphotypes are clearly not equivalent to modern botanical taxa, which are based on the features of the whole plant, especially the reproductive structures, rather than just fragmentary leaf material. They can, however, be compared to fossil form genera, which are also defined on the basis of visual determination of groupings, the only difference being that grouping is usually subjectively assessed by the researcher. Using a statistical approach and a computer, it is possible to take many characters into account simultaneously and make more objective decisions on grouping.

4.4.4.1 The advantages of a multivariate statistical approach

There have been calls for a coherent system of data banking of information on fossil angiosperm leaves since the 1950's (Dilcher 1974 and references cited therein, Spicer 1986b). Different researchers group, describe and identify fossil angiosperm leaves in different ways. This is a particular problem when angiosperm leaf taxa are identified and named in the literature, but no illustration or description with clear ranges of measurements and features is offered (e.g. Orlando 1964). In order to make comparisons with taxa that have already been described it may therefore be necessary to return to the original fossil specimens, if these are

available. Spicer (1986c) noted that there is a high degree of morphological plasticity in Cretaceous angiosperm leaves and that the whole range of features observed in each leaf of a taxon should be recorded. This is not generally possible with traditional taxonomic descriptions. The continuous nature of architectural variation could, however, be represented in data matrices of this kind and could accompany traditional taxonomic literature. The original raw data matrices for this study of Late Cretaceous Antarctic angiosperm leaves are included in Appendix 3, Table A3-1 and Table A3-2.

Within the data sets employed here there is much more information than is usually given in traditional descriptions of fossil material. This type of coding of a wide range of leaf architectural features allows a detailed account of the morphology to be stored in a concise format. This data can be placed on the Internet and downloaded by researchers wanting to make comparative studies of angiosperm leaves. This type of approach could improve access to the information on previously described fossils and multivariate statistical assessment of similarities may speed up the process of identifying similar groups of fossils on which to focus comparisons. Data on modern leaves could also be stored to allow relatively rapid comparison. Real benefits may come from combining data from living and fossil leaves and thus facilitating more objective identification. An example of this approach is that of Christophel (1985) who carried out numerical clustering analysis of extant and fossil *Nothofagus* leaves in order to assess similarities.

A multivariate statistical approach may also allow more objective grouping, since individual taxonomists may prefer either 'lumping' or 'splitting'. These issues arise in the study of both fossil and modern plant groups (Hall 1997). The subjectivity of isolating morphotypes is an important consideration in both palaeoclimate and biodiversity studies.

5 Descriptions of leaf morphotypes from the Cretaceous of the Antarctic Peninsula

5.1 Introduction

Following the work in previous chapters, 41 morphotypes from the Hidden Lake Formation and Santa Marta Formation were defined on the basis of visual and statistical means. In Chapter 3 the equivalence of these morphotypes to form genera has been discussed. In this chapter the individual morphotypes are formally described. The main characteristics are outlined and the range of features is noted. Possible affinities with fossil and living angiosperm leaves are then discussed.

There have been relatively few detailed studies of angiosperm leaves from the Cretaceous of Antarctica and these are the first leaf floras studied from these strata within the James Ross Basin. Comparisons with published literature on other fossil leaves are made, but literature on fossil angiosperm leaves from the Cretaceous of the Southern Hemisphere is sparse. Many of these morphotypes are compared with leaves described or illustrated from the Tertiary of the Antarctic Peninsula, supported by the work of Birkenmajer and Zastawniak (1989a) who noted that certain dicotyledonous angiosperm leaf taxa were persistent on the Antarctic Peninsula from the Late Cretaceous through to the early Oligocene. Critical comparisons with modern leaves have been made. However, these fossil floras are Cretaceous, at a relatively early stage in the evolution of the angiosperms and it is understood that the chance of identifying modern species in these fossil floras is quite slim. The discussion of affinities with modern species is given to illustrate the occurrences of particular characteristics rather than to confidently give a record of a particular taxon. It is also accepted that it is not possible to identify an angiosperm family using fragmentary leaf impressions alone. Confirmation of familial affinity requires examination of cuticular anatomy, which is lacking in this material. Although there are leaves with which no affinities can be discussed because of the degree of fragmentation, these are included because they form separate taxa and are useful in palaeoclimatic analyses.

The classification followed is generally that of Cronquist (1981), but to facilitate comparison with dicotyledonous angiosperm leaf studies, some exceptions have been adopted based on the leaf architectural studies of Hickey and Wolfe (1975). An example is the grouping of the Myrtales with the Dilleniidae rather than the Rosidae.

The computerised interactive identification key for Australian tropical rain forest trees (Hyland and Whiffin 1993) was of some assistance in the study of venation patterns of living angiosperms. However, its usefulness was limited because it only includes plants from a relatively small area of the world.

To facilitate comparison with published research on angiosperm leaves from the Antarctic, a database of the literature was designed and constructed using Microsoft Access with a

supporting application in VisualBasic. This database contains collection records of angiospermous fossils that have been previously documented. Where the relevant information is available, the leaf fossil records incorporate the principal venation pattern. A search using venation patterns enables a subset of the literature to be selected for more detailed comparison. This database was also used to collate information on the changing floral composition of the Antarctic Peninsula (see Chapter 7).

In this chapter, the Hidden Lake Formation and Santa Marta Formation leaves are described together for economy of space. There are many leaf forms that are similar in both floras, but any differences between leaves of the two different ages are recorded in the descriptions. There is a relatively large number of morphotypes and it is probable that with more complete preservation some of these groups could have been combined. The morphotype numbering is arbitrary and the morphotypes are listed in order of quantity of material rather than quality. The ratings in parenthesis following each specimen number are explained in Chapter 2. Each description refers to the features of the morphotype rather than specimens. These characteristics are a compilation of information from the specimens within that morphotype. Representative photographs of the majority of the morphotypes are included in Chapters 2 and 3. Each morphotype is illustrated in this chapter using a selection of specimens demonstrating the greatest number of characteristic features. Copies of the original drawings are presented in Appendix Volume 2, where colour is used to designate the different vein orders and thus display the venation patterns more clearly. In all of these figures, leaf outlines considered true margins are drawn as solid lines, while dotted lines are used to indicate where outlines are not considered true margins.

At the end of this chapter the main components of the Hidden Lake Formation and Santa Marta Formation floras are summarised. The implication of these floras in the context of research on the changing composition of the vegetation present on the Antarctic Peninsula during the Late Cretaceous is discussed in Chapter 7.

5.2 Morphotype descriptions

5.2.1 Morphotype 1
Figure 5.1. Plates 3.3A and 3.3B.

Specimen numbers

Hidden Lake Formation: Almost whole leaves: D8754.8.35a&37a (part and counterpart) (good), D8754.8.36a (good), D8754.8.40a (good), D8754.8.98a (excellent). Fragmentary leaves: D8754.8.98c (good), D8754.8.49a (fairly good), D8754.8.16a (fairly good), D8754.8.67a (fair), D8754.8.22a (fairly poor).

Santa Marta Formation: Almost whole leaf: D8618.106a (very good). Fragmentary leaves: DJ147.9a&15a (part and counterpart) (fairly good), DJ147.48a (fairly good), DJ147.60b (fairly good), DJ147.31a (fairly good), DJ147.60a (fairly good), D8605.8Aa&Ba (part and counterpart) (fairly good), DJ147.26a (fair).

Description

Lamina length 17.4-66.4mm min. Lamina width 15.5-36.6mm min. The lamina is asymmetrical and oblong, elliptic, or ovate, with an average length/width ratio of approximately 2.59:1 (range 1.74-4.12:1). Estimated leaf area 435-1557mm^2 min., microphyllous. Leaf organisation appears simple. Apex appears roughly symmetrical and is acute to attenuate (Figure 5.1c,d), with an average apical angle of approximately 61°. The base is asymmetrical or roughly symmetrical. Average basal angle is approximately 88° and base is acute to obtuse and normal, cuneate or decurrent (Figure 5.1b,e). A normal petiole is present (Figure 5.1e) and is approximately 0.7-2.2mm wide and 0.5-9.2mm in length. In D8754.8.49a (Appendix Volume 2 p115) the petiole is markedly curved. Margin is entire. Although there may be spines along the margin of D8618.106a (Figure 5.1b), the level of preservation of the leaf does not allow the confident description of spines.

Venation is pinnate camptodromous brochidodromous to eucamptodromous (Figure 5.1d). At the estimated leaf midpoint, the average primary vein width is approximately 0.56mm (range 0.26-1.02mm). The average size is 2.8% (range 1.29-4.7%) and is termed stout (Figure 5.1b,d). Primary vein course is either straight (Appendix Volume 2 p146) or curved (Figure 5.1a). There are up to 9-20 opposite or alternate pairs of secondary veins diverging from the midvein at angles of 27-104°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (63°, range 43-78°). Basal secondary veins diverge from midvein at a narrow to wide acute angle (40-79°, average 58°). Divergence angle appears nearly uniform in a few specimens but in most varies irregularly. Divergence angle is symmetrical in the most complete leaves, but is more acute on one side of the leaf than the other in some of the fragmentary specimens. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and either branched or unbranched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 100°) (Figure 5.1c). They also appear to be enclosed by secondary, tertiary, or quaternary arches. In

some of the specimens the secondaries gradually diminish rather than form prominent loops. In D8754.8.36a (Figure 5.1e), D8754.8.98a (Figure 5.1d), and D8754.8.98c (Appendix Volume 2 p146), it appears that in parts of the leaf the looping secondary veins may form an intramarginal vein but this is not clear. There appears to be simple intersecondary veins present (Figure 5.1a). The tertiary vein combination is AR (Figure 5.1d, Plate 3.3B, Appendix Volume 2 p136). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is similar to the average angle of tertiary divergence from the exmedial side of the secondary veins (Figure 5.1b). The tertiary vein pattern is random reticulate to weakly percurrent (Plate 3.3B, Appendix Volume 2 p136, Figure 5.1b,d). The higher order venation appears to form a reticulum in which vein orders cannot be distinguished (Appendix Volume 2 p136). Marginal ultimate venation is looped (Figure 5.1c).

Differential characters

This leaf type is the most abundant and is distinguished by its pinnate camptodromous brochidodromous to eucamptodromous venation (Figure 5.1d), entire margin and petiolate base (Figure 5.1e). It is differentiated from other leaves with the same venation type within these floras by the oblong, elliptic or ovate lamina form and the moderate acute angle of divergence of the basal secondary veins (Figure 5.1d).

Discussion

Entire margined leaves with camptodromous brochidodromous venation occur within many angiosperm groups and are found within the Magnoliidae, Hamamelidae, Caryophyllidae, Dilleniidae and Rosidae (Hickey and Wolfe 1975). However, in most of the Cretaceous fossil specimens of Morphotype 1 the secondary and higher order veins have an irregular course and the intercostal areas are not uniform in size and shape. In some cases the leaf bases are also decurrent (Figure 5.1e). These are features of leaves of the first rank (Hickey 1977) and are typical of the Magnoliales, with similar forms occurring in the Winteraceae and Annonaceae.

Dutra *et al.* (1998) recorded leaves with brochidodromous venation with possible affinities to the Magnoliidae, Dilleniidae or Rosidae from the Campanian of Nelson Island, South Shetland Islands, but the photograph is too poorly reproduced to allow comparison. Dusén (1908) also illustrated several leaf forms with a similar shape, entire margin, and venation pattern as *Phyllites* sp. 12, *Phyllites* sp. 21, *Phyllites* sp. 24, and *Phyllites* sp. 25 from the Tertiary of Seymour Island. Zastawniak (1994) described fragmentary leaves with brochidodromous venation from the Santonian-Maastrichtian of King George Island, South Shetland Islands, as *Magnoliidaephyllum birkenmajeri* with suggested affinities to the Magnoliidae. The leaves of *M. birkenmajeri* are too fragmentary for detailed comparison with Morphotype 1, since the apices, bases and margins are not preserved in the King George Island specimens. The venation pattern does show some similarity to that observed in Morphotype 1, with a stout midvein, secondary veins diverging from the midvein at a moderate acute angle and tertiary vein combination of AR. However, the two leaf forms differ in secondary and tertiary vein pattern,

since in *M. birkenmajeri* the secondary veins join the superadjacent secondaries at an approximate right angle and the tertiary veins are percurrent with an approximately right-angled relationship to the midvein. Leaves of the Winteraceae are considered to be of the first rank (Hickey 1977) and a leaf described as *Drimys antarctica* (Winteraceae) from Seymour Island by Dusén (1908) appears similar to these James Ross Island leaves. However, although they show a similar type of venation, modern and fossil leaves of this genus, e.g. *Drimys patagonica* described by Berry (1938) from the Tertiary of Argentina, tend to be obovate, which is not the case for the James Ross Island leaves. Zastawniak (1994) also described a leaf from the Santonian-Maastrichtian of King George Island as *Dicotylophyllum* sp. 11 with suggested affinities to the Winteraceae. The King George Island leaf is described as possessing probable brochidodromous venation and a stout primary vein with irregular secondary and tertiary veins. These features are similar to those observed in Morphotype 1 but *Dicotylophyllum* sp. 11 is too poorly preserved for detailed comparison with Morphotype 1.

The irregularly looping secondary veins observed in Morphotype 1 indicate that botanical affinities may lie with the Magnoliales. Although the leaves of Morphotype 1 cannot confidently be assigned to the Winteraceae, there is support for the existence of this family on the Antarctic Peninsula during the deposition of the Santa Marta Formation from new records of fossil wood (Poole and Francis 2000).
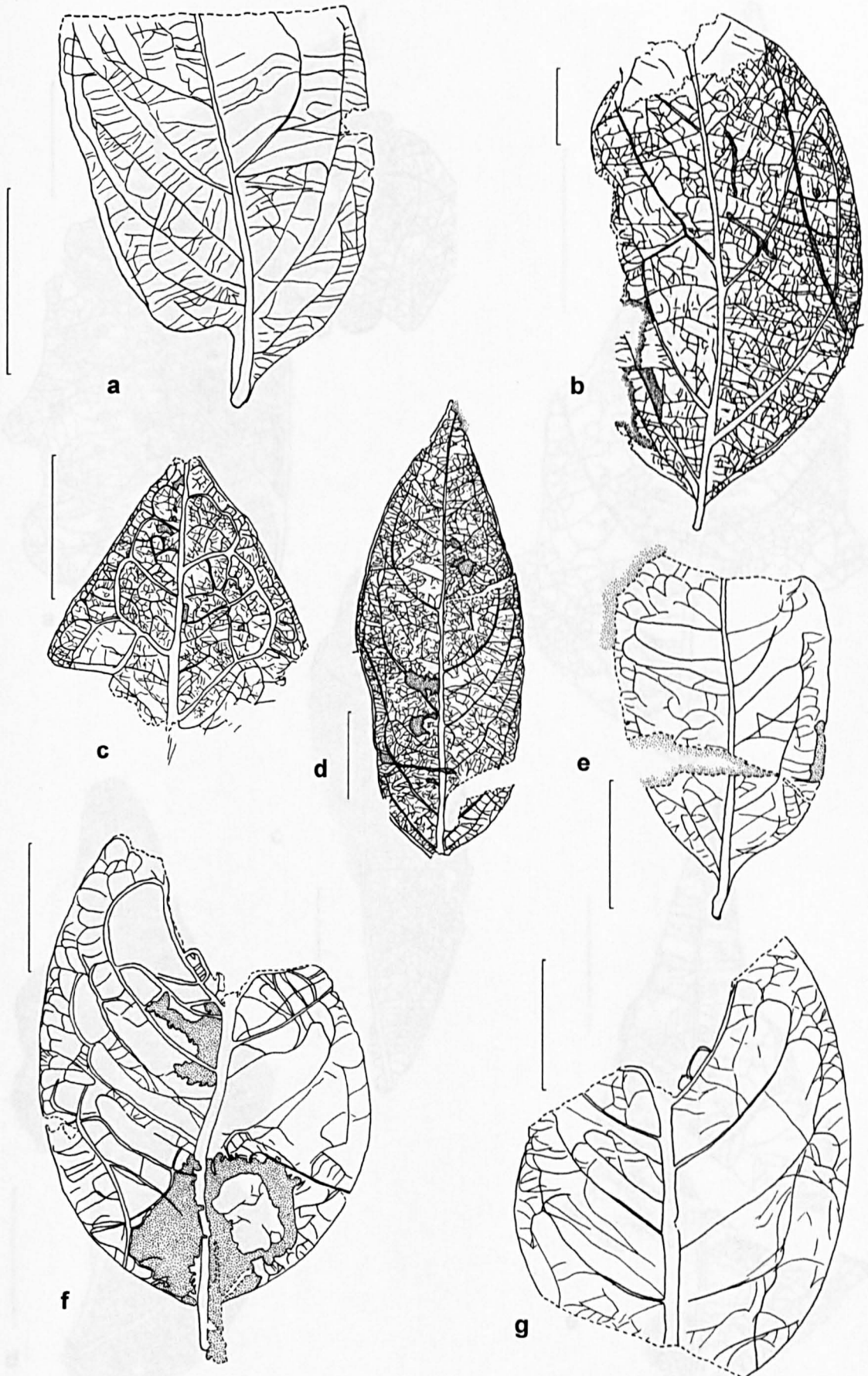
Figure 5.1 Morphotype 1. (a) D8754.8.40a. (b) D8618.106a. (c) DJ147.15a.
(d) D8754.8.98a. (e) D8754.8.36a. (f) D8754.8.35a. (g) D8754.8.37a.
Scale bar is 10mm.
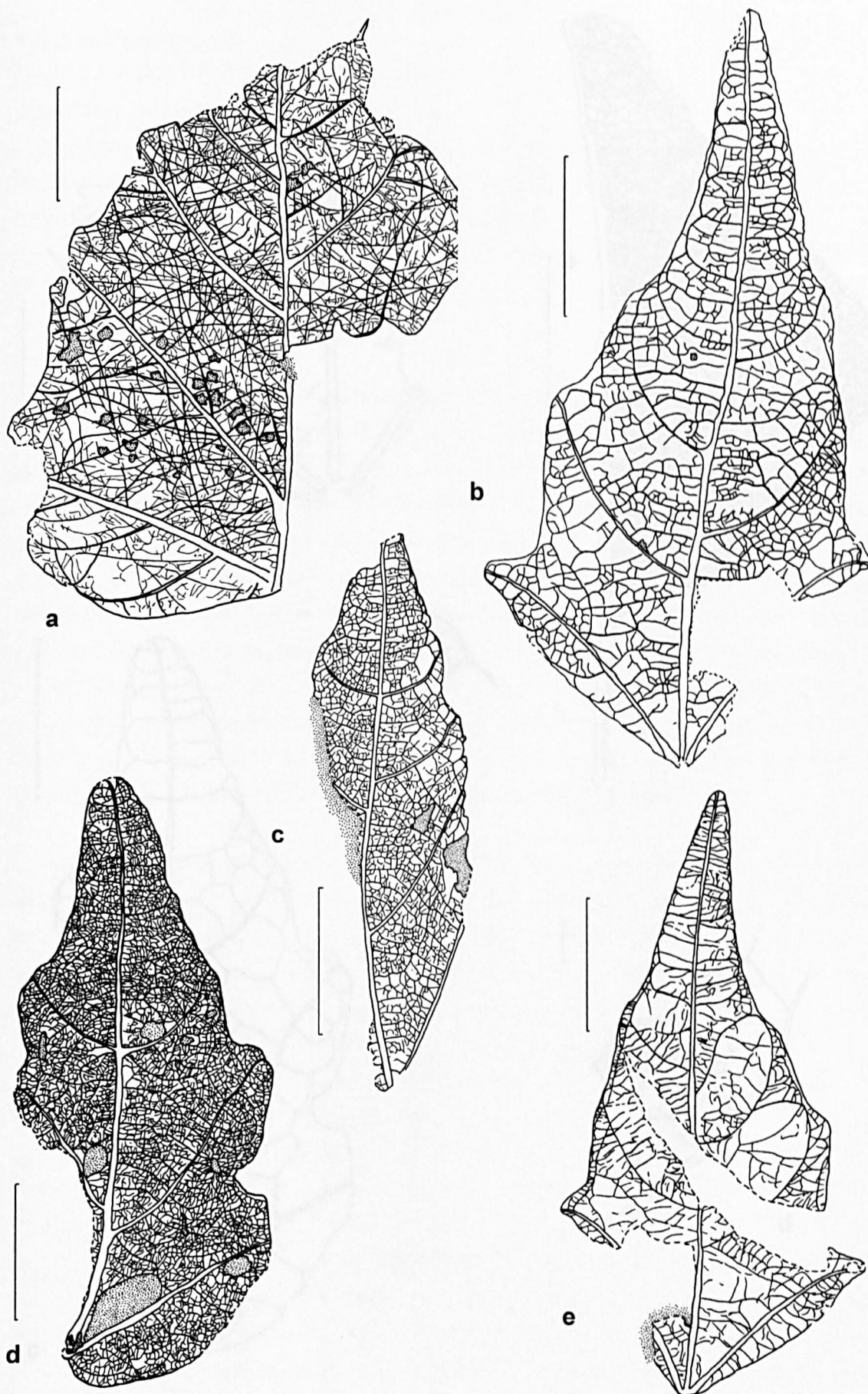
**Figure 5.2 Morphotype 2. (a) D8754.8.100a. (b) D8754.8.3a. (c) DJ147.11a.
(d) D8754.8.1a. (e) D8754.8.2a.
Scale bar is 10mm.**
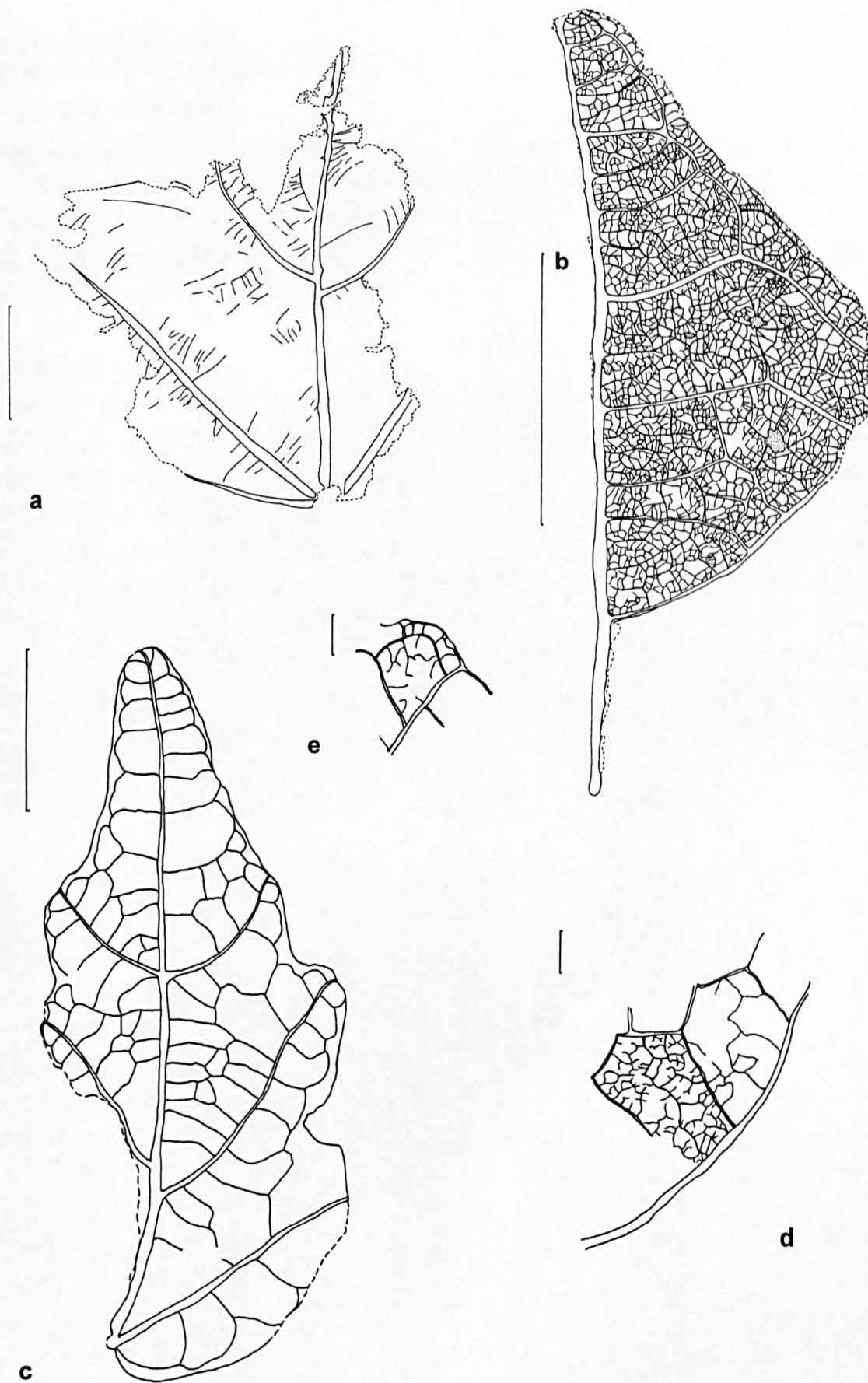
Figure 5.3 Morphotype 2. (a) D8754.8.61a. (b) D8754.8.27a.
(c) Simplified drawing of D8754.8.1a. (d) D8754.8.1a. (e) D8754.8.1a margin.
Scale bar is 10mm in (a), (b) and (c). Scale bar is 1mm in (d) and (e).

5.2.2 Morphotype 2
Figure 5.2, Figure 5.3. Plates 3.4A, 3.3D, 2.2D.

Specimen numbers

<u>Hidden Lake Formation</u>: Almost whole leaves: D8754.8.1a (excellent), D8754.8.2a&3a (part and counterpart) (excellent). Fragmentary leaves: D8754.8.100a (fairly good), D8754.8.61a (fairly good), D8754.8.27a (fairly good), D8754.8.58a (fairly good).

<u>Santa Marta Formation</u>: Fragmentary leaves: DJ147.11a (excellent), D8619.12a (very good), DJ147.23a (fairly good), DJ147.20a (good).

Description

Lamina length 19.1-67.2mm min. Lamina width 12.1-90.8mm min. Using measurements from almost complete specimens, lamina is slightly asymmetrical and ovate (Figure 5.2b,d,e), with the point of maximum width 26% of the distance from the leaf base. The average length/width ratio is 1.98:1. Estimated leaf area 193-10883mm^2 min., microphyllous to mesophyllous. Leaf organisation appears to be simple. Apex appears roughly symmetrical and is attenuate (Figure 5.2b,d,e), with an average apical angle of 52°. Base appears to be slightly asymmetrical and is obtuse cuneate (Figure 5.2b,e) or cordate (Figure 5.2d) with an average basal angle of approximately 133°. Petiole absent or not preserved. Margin is non-entire, indented at least 0.4-2.8mm, average 1.7mm min., approximately 13% of distance to midvein. Apices of projections are rounded, so the margin is described as crenate (Figure 5.2b,d,e). Sinuses are rounded. Spacing of crenations is 4.4-27.5mm, average 12.2mm. For each leaf, standard deviation of spacing measurements is 1.8-2.6mm and spacing is described as irregular.

Venation basal, marginal imperfect actinodromous (Figure 5.2b,d,e, Figure 5.3a), with three to five primary veins diverging from the leaf base. The veins originating on the lateral actinodromous primary veins cover a maximum of 50% of the blade area. Lateral primaries diverge from the base at an average angle of 45° to the midvein (range 27-82°). In the apical part of the leaf the secondary veins are camptodromous brochidodromous (Figure 5.2b,c,d,e). D8619.12a (Appendix Volume 2 p247) may have palinactinodromous venation but the leaf is very fragmentary thus hindering certain determination. At the estimated leaf midpoint, the average primary vein width is 0.48mm (range 0.28-0.87mm). The average size is 1.93% (range 1.13-2.66%) and is termed moderate (Figure 5.2d). Primary course is markedly curved (Figure 5.2d). The primary vein only appears to be straight in the specimens with parts of the leaf missing e.g. D8754.8.100a (Figure 5.2a) and DJ147.23a (Appendix Volume 2 p284). There are up to 9-10 opposite or alternate pairs of secondary veins diverging from the midvein at angles of 36-124°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is wide acute (70°, range 44-89°). Basal secondary veins diverge from midvein at a narrow to wide acute angle (44-75°, average 58°). In some specimens the lowest pair of secondary veins is more acute than all those above (Figure 5.2c,d), while in others the divergence angle varies irregularly. Divergence angle is more acute on one side of the midvein than the other in the most complete specimens, appearing symmetrical in more fragmentary

material. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and unbranched. In the middle part of the leaf, secondary veins terminate at the centre of crenations, while in the apical part they form loops (Figure 5.2d, Figure 5.3c). Loop-forming branches join the superadjacent secondary at an obtuse angle (average 121°). They also appear to be enclosed by secondary, tertiary, or quaternary arches (Figure 5.2b,c,d,e). There may be composite intersecondaries present in some specimens (Figure 5.3b). The tertiary vein combination is RR (Figure 5.2b,c,d, Figure 5.3c). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is approximately equal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is random reticulate to weakly percurrent. The course of the percurrent tertiaries is forked, sinuous, and recurved. The tertiaries show an oblique relationship to the midvein, trending in an obtuse angle, decreasing apically. Their arrangement is predominantly alternate and closely spaced, with 4-5 veins/cm (Figure 5.2c,d, Figure 5.3c). The higher vein orders are distinct. The quaternaries and quinternaries are relatively randomly oriented (Figure 5.2d, Figure 5.3d). The marginal ultimate venation is looped (Figure 5.2d, Figure 5.3e). The quaternary areolation appears imperfect, randomly arranged, irregularly shaped and medium sized (0.5-1mm).

Differential characters

This morphotype is clearly distinguished from all other leaves within these floras by the possession of actinodromous venation and a crenate margin (Figure 5.2b,d,e, Figure 5.3a, Plates 3.4A, 3.3D). It is also differentiated from other morphotypes with this type of venation by the presence of a cordate (Figure 5.2d) or obtuse cuneate base (Figure 5.2b,e), an attenuate apex (Figure 5.2e), and wide acute secondary vein divergence from the midvein (Figure 5.3c).

Discussion

Recent leaves with actinodromous venation of this type are known from the Dilleniidae, Hamamelidae and Rosidae, but the weakly percurrent tertiaries concentrically oriented with respect to the petiole observed in Morphotype 2 (Figure 5.3c) is characteristic of the palmate Dilleniids (Hickey and Wolfe 1975). Within this subclass, the Malvales (e.g. Bombacaceae, Elaeocarpaceae, Sterculiaceae, Tiliaceae) and some Violales (e.g. Bixaceae) possess teeth without glands that appear to be the closest to the marginal processes of Morphotype 2 (Figure 5.2b,d,e).

Within Late Cretaceous strata of the Antarctic Peninsula some leaves with actinodromous venation have been referred to *Cochlospermum* (Bixaceae) (Birkenmajer and Zastawniak 1986, 1989b). Modern species of *Cochlospermum* show similarities to Morphotype 2 but are either clearly palmately lobed or show a zone of interaction possibly indicating the fusion of palmate lobes (Klucking 1995). These features are not observed in Morphotype 2. The fossil material illustrated by Birkenmajer and Zastawniak (1986, 1989b) is too poorly preserved to allow close

comparison but it differs from Morphotype 2 in that it has a lobed margin and seven primary veins diverging from the base of the leaf.

Many modern species of the Sterculiaceae, e.g. *Lasiopetalum floribundum* and *Brachychiton grandiflorus* from Australia, are characterised by actinodromous venation and do not have lobes, which is in accordance with these fossils, in addition to a similar apical and basal style to Morphotype 2. Birkenmajer and Zastawniak (1989b) and Li (1994) recorded leaves with actinodromous venation of *Sterculia*-type from the Paleocene-Eocene Dufayel Island and Fildes Peninsula floras from King George Island, South Shetland Islands. These leaf impressions were formally described as *Dicotylophyllum latitrilobatum* by Birkenmajer and Zastawniak (1989a) with suggested affinities to the Hamamelidae or Dilleniidae (possibly *Cochlospermum* or *Sterculia*). They are palmately tri-lobed with perfect basal marginal actinodromous venation. Similar leaves were described as *Phyllites* sp. 9 by Dusén (1908) from Tertiary strata of Seymour Island and *Sterculia* by Czajkowski and Rösler (1986) from the Tertiary of King George Island. The venation pattern of *D. latitrilobatum*, with three primary veins radiating from the leaf base, is similar to Morphotype 2, except that while in *D. latitrilobatum* the development of the actinodromous venation is described as perfect, in Morphotype 2 the development is imperfect. Other similarities are the obtuse base, the acute attenuate apex and the random reticulate tertiary venation pattern. Differences to Morphotype 2 include the stout size of the primary veins and moderate acute divergence of the secondary veins in *D. latitrilobatum*. The secondaries in *D. latitrilobatum* are brochidodromous, but in Morphotype 2 the lower secondaries reach the leaf margin and terminate at the centre of crenations and only form loops in the apical part of the leaf. These loop-forming branches also differ in the angle at which they join the superadjacent secondary, right-angled in *D. latitrilobatum*, but obtuse in Morphotype 2. The main difference between the leaves discussed above and those of Morphotype 2 is that the King George Island specimens have lobed margins and the James Ross Island specimens have a crenate margin. However, it is possible that one of the specimens studied, D8754.8.61a (Figure 5.3a), may have a lobed margin, but the specimen is too fragmentary for a confident determination. The almost whole leaves studied here which show the well preserved crenate margin are rather small in comparison to the fragmentary specimens. It is possible that these almost whole leaves might be juvenile leaves as it appears that the development of lobes is seen only in the relatively more mature sterculiaceous leaves (pers. obs.).

Leaf fossils with suggested affinities to the Sterculiaceae were also recorded by Orlando (1964) as *Sterculia washburnii* and *Sterculia patagonica* from the Tertiary of King George Island, but no description or illustration was provided preventing comparison. Sterculiaceous leaf fossils documented from the Late Cretaceous-Tertiary of King George Island (Dutra 1989) are too poorly preserved for detailed comparison. Records from the Late Cretaceous of Patagonia (Berry 1937c) and the Tertiary of Argentina (Berry 1938) are not considered similar enough, architecturally, to Morphotype 2 to warrant further comparison.

From the overall architectural characters closest affinity with Morphotype 2 seems to lie with the Sterculiaceae but affinity with the Bixaceae and in particular *Cochlospermum* cannot be ruled out. Moreover, Sterculiaceae (Malvales) and Bixaceae (Violales) may be very closely related as they share chemical composition of their gums (Cronquist 1981).

5.2.3 Morphotype 3

Figure 5.4a,b,c,d,e. Plates 3.4B and 3.10D.

Specimen numbers

Hidden Lake Formation: Almost whole leaves: D8754.8.33a (fairly good), D8754.8.45a (excellent). Fragmentary leaves: D8754.8.46a (good), D8754.8.68a (good), D8754.8.76b (fairly good), D8754.8.5d (fairly poor), D8754.8.59c (fair).

Santa Marta Formation: Fragmentary leaves: D8619.7a (good), D8605.5a&15a (part and counterpart) (fairly good), D8606.4Aa&Ba (part and counterpart) (fairly good).

Description

Lamina length 21.5-54.2mm min. Lamina width 12.2-30.2mm min. The lamina is slightly asymmetrical and wide obovate. Using measurements from almost complete specimen, D8754.8.45a (Figure 5.4a), length/width ratio is 1.91:1. Estimated leaf area 208-1161mm^2 min., microphyllous. Leaf organisation appears simple. Apex appears slightly asymmetrical and is acute (Figure 5.4a), with an apical angle of approximately 38°. Base appears to be asymmetrical or symmetrical. Average basal angle is approximately 51° and base is acute decurrent (Figure 5.4a,c). A normal petiole is present (Figure 5.4a,c) and is approximately 0.6-1.8mm wide and at least 1-9mm in length. In D8754.8.5d (Appendix Volume 2 p67) the petiole appears to be winged, but this specimen is not clearly preserved. Margin is entire (Figure 5.4a,b).

Venation is pinnate camptodromous brochidodromous to eucamptodromous (Figure 5.4a). At the estimated leaf midpoint, the average primary vein width is approximately 0.72mm (range 0.45-0.97mm). The average size is 5.02% (range 2.74-10.42%) and is termed massive (Figure 5.4c). Primary vein course is straight (Figure 5.4a). There are up to 8 opposite or alternate pairs of secondary veins diverging from the midvein at angles of 12-84°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (52°, range 38-69°). Basal secondary veins diverge from midvein at a narrow to moderate acute angle (12-62°, average 33°) (Figure 5.4a). In most specimens the lowest pair of secondary veins is more acute than all those above (Figure 5.4a), while in others the divergence angle varies irregularly (Appendix Volume 2 p109). Divergence angle is more acute on one side of the leaf than the other, only appearing symmetrical in the most fragmentary specimens. The secondary veins appear to be relatively fine to moderate. The course of the secondaries is abruptly curved and branched, with only the most incomplete specimens not demonstrating secondary branching. Loop-forming branches join the superadjacent secondary at an approximate right angle (average 83°). They also appear to be enclosed by secondary, tertiary,

or quaternary arches (Figure 5.4a,b). It appears that looping secondaries may form an intramarginal vein in part of the most complete specimen, D8754.8.45a (Figure 5.4a), but this is not clear. In D8754.8.45a there are enclosing arching secondaries segmented by branching secondary veins. These secondary arches follow the outline of the leaf. There are composite intersecondary veins present (Figure 5.4a,d). The tertiary vein combination is AR (Figure 5.4a). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an acute angle, with an average which is similar to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is random reticulate to weakly percurrent (Figure 5.4a,b,e). The higher vein orders are distinct. The quaternary veins and quinternary veins are relatively randomly oriented (Figure 5.4e). Marginal ultimate venation is looped, but may form a fimbrial vein in the basal part of the leaf (Figure 5.4d). Quaternary areolation is imperfect, randomly oriented, irregularly shaped and large in size (1-2mm) (Figure 5.4e).

Differential characters

This leaf type is distinguished by its pinnate camptodromous brochidodromous to eucamptodromous venation, entire margin and acute decurrent petiolate base (Figure 5.4a, Plate 3.4B). It is differentiated from other leaves with the same venation type within these floras by the obovate form (Figure 5.4a) and massive primary vein (Figure 5.4c). The basal secondary vein divergence from the midvein is narrow acute while the divergence of the secondaries above is moderate acute (Figure 5.4a). A further difference is the acute angle of origin of tertiary veins on the midvein (Figure 5.4a,b,e).

Discussion

Entire margined leaves with camptodromous brochidodromous venation occur within many angiosperm groups and are found within the Magnoliidae, Hamamelidae, Caryophyllidae, Dilleniidae and Rosidae. The acute decurrent leaf base, irregularly brochidodromous venation in ascending arches, acute decurrent basal secondary veins and weakly percurrent tertiary veins are, however, particularly characteristic of the Santalales (Dilleniidae) (Hickey and Wolfe 1975).
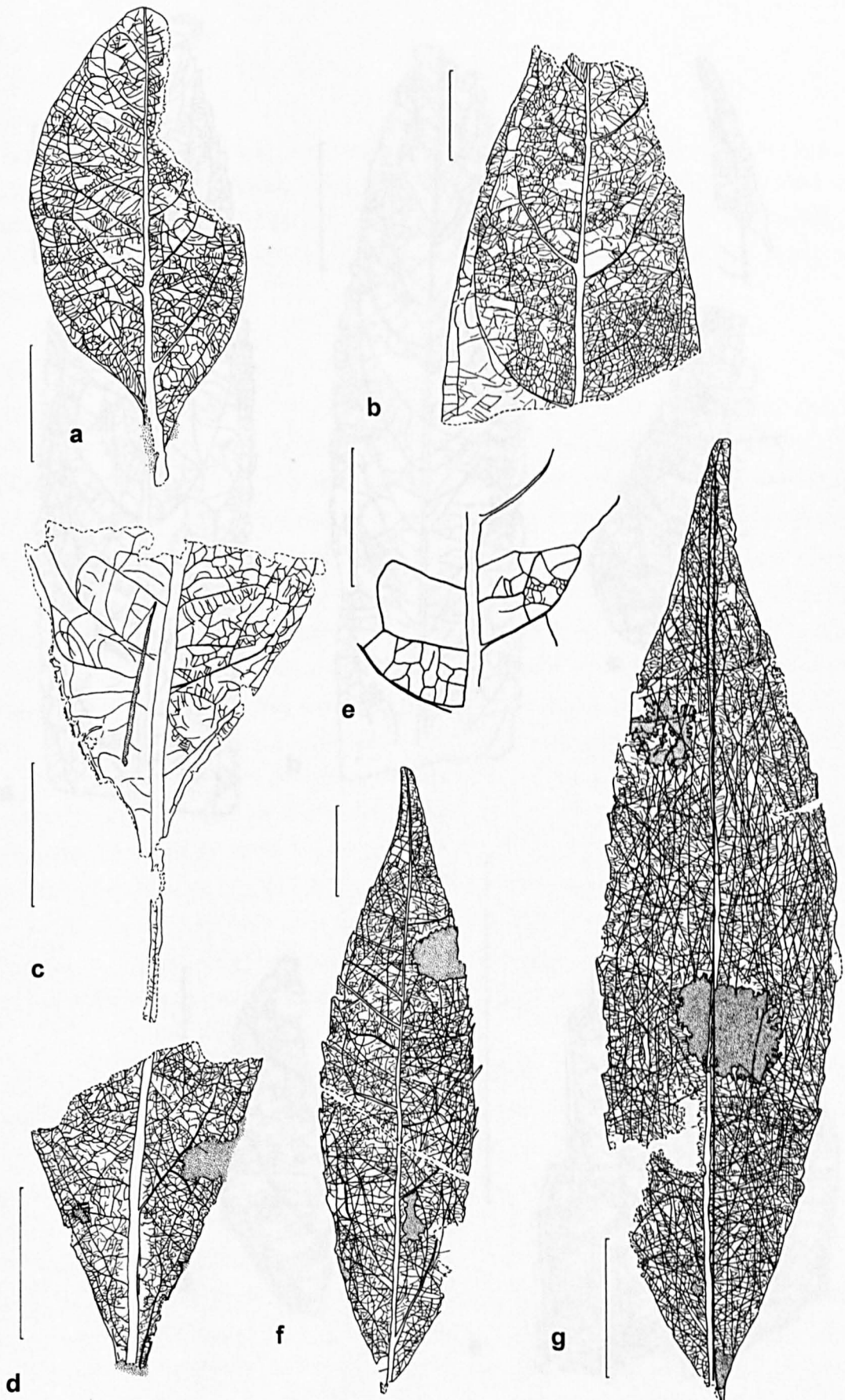
Figure 5.4 Morphotype 3. (a) D8754.8.45a. (b) D8619.7a. (c) D8754.8.33a.
(d) D8754.8.68a. (e) D8619.7a.
Morphotype 4. (f) DJ134.15Ba. (g) DJ134.15Aa. Scale bar is 10mm.
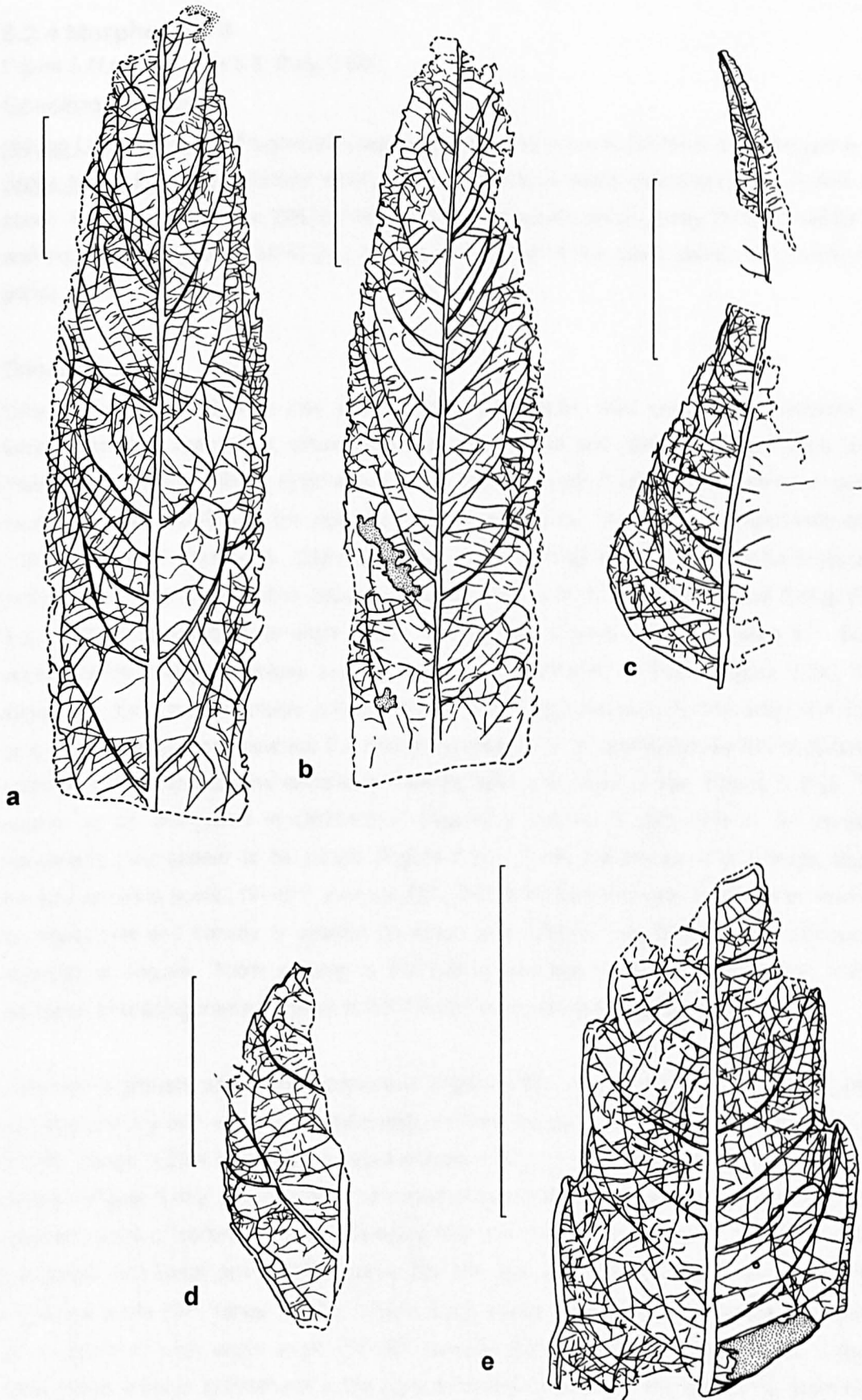
Figure 5.5 Morphotype 4. (a) D8606.7Aa. (b) D8606.7Ba. (c) DJ147.44a.
(d) DJ147.41Aa. (e) DJ147.24a.
Scale bar is 10mm.

5.2.4 Morphotype 4

Figure 5.4f,g and Figure 5.5. Plate 3.5A.

Specimen numbers

<u>Hidden Lake Formation</u>: Fragmentary leaves: D8754.8.17b (poor), D8754.8.4d (fairly good).

<u>Santa Marta Formation</u>: Almost whole leaves: DJ134.15Aa&Ba (excellent), DJ147.44a (very good). Fragmentary leaves: D8606.7Aa&Ba (part and counterpart) (good), DJ134.2Aa&Ba (part and counterpart) (good), DJ147.24a (fairly good), DJ147.41Aa (fairly good), DJ134.28a (fairly good).

Description

Lamina length 17.9-69.8mm min. Lamina width 9.2-41.4mm min. Using measurements from almost complete specimens, whole lamina is symmetrical and narrow oblong (Figure 5.5a,b, Plate 3.5A), narrow elliptic (Figure 5.4f,g) or narrow ovate (Figure 5.5c), with the point of maximum width 18-49% of the distance from the leaf base. The average length/width ratio is 3.27:1 (range 2.71-3.83:1). Estimated leaf area 185-3736mm^2 min., microphyllous to notophyllous. Leaf organisation appears to be simple. Apex is attenuate (Figure 5.4f,g, Figure 5.5c), with an average apical angle of 34°. Average basal angle is approximately 81°. Base is acute (Figure 5.4f,g) to obtuse and appears to be normal or rounded (Figure 5.5c). There appears to be a normal petiole present (Figure 5.5c), approximately 0.4mm wide and 0.5mm long. Margin is toothed, indented 0.1-1.8mm, average 0.5mm, approximately 8% of distance to midvein. Size of projections decreases towards apex and base of leaf (Figure 5.4f,g). Teeth appear to be compound in D8754.8.4d (Appendix Volume 2 p66), but in the remaining specimens they appear to be simple (Figure 5.5e). Teeth are serrate and average angle of pointed apices is acute (15-167°, average 89°). Dominant serration type is convex or acuminate on basal side and convex or straight on apical side (Figure 5.4g, Figure 5.5e). Sinuses are rounded or angular. Tooth spacing is 0.2-6.2mm, average 2.7mm. For each leaf, standard deviation of spacing measurements is 0.2-1.6mm and spacing is described as irregular.

Venation is pinnate semicraspedodromous (Figure 5.5d). At the estimated leaf midpoint, the average primary vein width is approximately 0.47mm (range 0.25-1.03mm). The average size is 3.27% (range 2.23-4.24%) and is stout (Figure 5.4f,g, Figure 5.5c). Primary vein course is straight (Figure 5.4f,g, Figure 5.5a,b) or curved (Figure 5.5c). There are up to 15 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 14-107°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (58°, range 50-66°) (Figure 5.5a). Basal secondary veins diverge from midvein at a narrow to wide acute angle (37-73°, average 50°). Divergence angle varies irregularly. Divergence angle is symmetrical in the most complete specimens, only appearing asymmetrical in some fragmentary leaves. The secondary veins appear relatively fine to moderate. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 103°) (Figure 5.5e). In DJ147.44a (Figure 5.5c), D8606.7Aa&7Ba (Figure 5.5a,b) and DJ147.24a (Figure 5.5e) the looping

secondaries alternate with secondaries reaching the margin. There appears to be simple intersecondary veins present (Figure 5.5a,b,e). The tertiary vein combination is AR (Figure 5.5a). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle with an average which is similar to the average angle of tertiary divergence from the exmedial side of the secondary veins. Tertiary vein pattern is random reticulate to weakly percurrent. Preservation levels do not allow higher order venation to be distinguished. There is no evidence of darker material, which may have indicated glands, in the tooth apices, but apices appear simple to papillate (Figure 5.5e). The principal vein of the tooth is a secondary, whose course is eccentric, tending to run along the apical side of the tooth, and is deflected.

Differential characters

This morphotype is distinguished from other leaves within these floras by the possession of pinnate semicraspedodromous venation and a toothed margin (Figure 5.5d). It is also differentiated from Morphotype 20, showing this type of venation, by the presence of an attenuate apex (Figure 5.4f,g, Figure 5.5c) and moderate acute secondary vein divergence from the midvein (Figure 5.5a). The Hidden Lake Formation leaves are poorly preserved as fragmentary patchy and uneven carbonaceous impressions.

Discussion

The teeth of this morphotype appear to be cunonioid (Figure 5.5e), with glandular apices and with the principal vein to each tooth branching below it, sending one branch to the superadjacent secondary vein and the other to the tooth apex along its apical side (Hickey and Wolfe 1975). Cunonioid teeth, along with the semicraspedodromous venation and percurrent tertiaries observed in these fossils (Figure 5.5d), are characteristic of Rosid orders such as the Saxifragales, Sapindales, Rhamnales (Leeaceae) and Oleales. Hickey and Wolfe (1975) stated that the leaves of the Rosales have rosoid teeth. According to Cronquist (1981), this order includes the Cunoniaceae, which possess cunonioid teeth. However, Cutler and Gregory (1998) include the Cunoniaceae within the Saxifragales. Figure 5.24a is a line drawing of herbarium material of the Cunoniaceae (*Ackama rosafolia*) which shows a similar tooth style and venation pattern to Morphotype 4.

Cantrill and Nichols (1996) described leaves of a very similar shape to some of these James Ross Island specimens from the late Albian of Alexander Island as *Ficophyllum palustris*. The size, leaf form, apical and basal style, tooth size and shape, primary vein size and secondary vein divergence from the midvein are all similar to Morphotype 4. However, the description of *F. palustris* states that, despite relatively good preservation, the secondary veins form loops with no evidence of branches leading to the teeth, which is not consistent with these James Ross Island leaves. Rees and Smellie (1989) figured a narrow elliptic leaf (Form E) with semicraspedodromous venation and a serrate margin from Williams Point on Livingston Island, South Shetland Islands, dated as Cenomanian-Campanian by Chapman and Smellie (1992).

These specimens are not very well preserved but the photograph shows that the secondaries arise from the midvein at a more obtuse angle and are more regular than in Morphotype 4. The leaf form described as *Monimiophyllum antarcticum* from the Tertiary of King George Island (Birkenmajer and Zastawniak 1989a) shows similarity of form to Morphotype 4, with semicraspedodromous venation and a toothed margin. However the secondary veins diverge from the midvein at a different angle and the tooth type is considered monimioid in *M. antarcticum*. One of the most similar leaves to Morphotype 4 from the Antarctic Peninsula is a form referred to *Myrica* from the Tertiary of King George Island (Czajkowski and Rösler 1986) and Argentina (Berry 1938). This leaf has a similar shape, apical and basal style, venation pattern, angles formed by secondary veins, and tertiary venation pattern. The teeth are also of a similar shape, but details of higher order venation and tooth architecture cannot be seen and the teeth appear larger in relation to leaf width in the Tertiary specimens illustrated. Despite the similarities, the leaves from James Ross Island do not appear to have the tooth type characteristic of the Myricales (compare Hickey and Wolfe 1975). Dusén (1908) also described other leaves with a similar shape, margin or venation pattern to the James Ross Island specimens as *Phyllites* sp. 14, 19, 22, and 23, but these are too poorly preserved and fragmentary for comparison.

From the Tertiary of King George Island, Czajkowski and Rösler (1986) and Li (1994) recorded leaves as *Rhoophyllum* with suggested affinities to the Anacardiaceae. These leaves have many similar features to Morphotype 4, including size, shape, apical and basal style, venation pattern and angles formed by the secondary veins, but from the illustrations, the teeth appear to be fairly large in relation to leaf size and are a different shape. Dusén (1908) recorded leaves of *Caldcluvia mirabilis* assigned to the Cunoniaceae from the Tertiary of Seymour Island. However, the illustrations of this material show that although the venation is similar, the shape of the leaf and the teeth are different to Morphotype 4, with one large tooth on either side of apical part of the lamina. Czajkowski and Rösler (1986) also described specimens assigned to *Caldcluvia mirabilis* from the Tertiary of King George Island. From their drawings it appears that these leaves have a similar form, basal style, similarly shaped serrations and semicraspedodromous venation with random reticulate tertiary veins, but these leaves are also different to Morphotype 4. They are very small, with an acute apex, very large teeth in relation to the leaf size and more irregular secondary venation forming different angles to those in Morphotype 4. However, these leaves recorded as *C. mirabilis* have subsequently been renamed as *Lomatia mirabilis* by Li (1994) who suggested that these leaves and others from the Tertiary of King George Island showed closer affinities to the Proteaceae. Zastawniak (1994) described a cunoniophyll morphotype from the Santonian-Maastrichtian of King George Island as *Dicotylophyllum* sp. 6. This leaf has a toothed margin but is too poorly preserved for any further comparison with Morphotype 4. One of the most similar leaf forms to Morphotype 4 is *Dicotylophyllum elegans* described from the Tertiary of King George Island by Li (1994). This leaf has a similar form, basal and apical style to Morphotype 4 with semicraspedodromous venation and cunonioid teeth. *D. elegans* also shares a stout midvein, subopposite secondary veins diverging from the

midvein at a moderate acute angle, intersecondary veins and random reticulate tertiary veins, but the looping tertiary veins along the margin are not observed in Morphotype 4.

Support for the presence of Cunoniaceae within Cretaceous Antarctic Peninsula floras comes from fossil wood most similar to modern *Weinmannia* within strata of the Hidden Lake Formation and Santa Marta Formation (Poole *et al.*, in press a). This wood is also recorded from the Cenomanian-Campanian of Livingston Island (Poole *et al.*, in press a), as is a form considered similar to *Ackama* (Dicotwood-Cretaceous-heterorays) (Chapman and Smellie 1992).

5.2.5 Morphotype 5
Figure 5.6a,b,c,d.
Specimen numbers
Hidden Lake Formation: Fragmentary leaf: D8754.8.7a (fairly good).
Santa Marta Formation: Almost whole leaves: DJ147.10a (excellent), DJ147.32a (excellent). Fragmentary leaves: DJ147.25a (good), DJ147.40a (fairly good).

Description
Lamina length 29-51.7mm min. Lamina width 12-26mm min. The lamina is asymmetrical and oblong to elliptic. Using measurements from most complete specimen, DJ147.10a (Figure 5.6a), length/width ratio is estimated to be 2.71:1. Estimated leaf area 260-1221mm^2 min., microphyllous. Leaf organisation appears simple. Apex appears to be attenuate (Figure 5.6a,c) and apical angle is estimated to be approximately 44°. Base is asymmetrical and acute (Figure 5.6a) to obtuse cuneate (Figure 5.6b), with an average basal angle of approximately 83°. Petiole absent or not preserved. Margin is entire (Figure 5.6a,c).

Venation is pinnate camptodromous brochidodromous (Figure 5.6a,b). At the estimated leaf midpoint, the average primary vein width is approximately 0.5mm (range 0.26-0.59mm). The average size is 2.42% (range 2.17-2.69%) and is stout (Figure 5.6a,b,c). Primary vein course is curved (Figure 5.6a). There are up to 12 pairs of secondary veins, opposite in the apical part of the leaf and alternate over the rest of the lamina. The overall range in secondary vein divergence is 20-104°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is wide acute (70°, range 52-77°) (Figure 5.6a). Basal secondary veins diverge from midvein at a moderate acute angle (50-56°, average 53°) (Figure 5.6b). Divergence angle varies irregularly and is either symmetrical or asymmetrical. The secondary veins are of moderate thickness. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an approximate right angle (average 84°). They also appear to be enclosed by secondary or tertiary arches (Figure 5.6a). There appears to be intersecondary veins present but it is not clear whether these are simple or composite (Figure 5.6a,b). The tertiary vein combination is RR (Figure 5.6d). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average angle which is similar to the average

angle of tertiary divergence from the exmedial side of the secondary veins. Tertiary venation pattern is random reticulate (Figure 5.6d). Higher order venation cannot be clearly distinguished but marginal ultimate venation appears to be looped (Figure 5.6a,c).

Differential characters

Morphotypes 5 and 10 are very similar, both having pinnate camptodromous brochidodromous venation, entire margins and attenuate apices (Figure 5.6a,b,c). However, the differences include the basal style, which is cuneate in this morphotype (Figure 5.6a,b) and acute normal to decurrent in Morphotype 10, the variation in secondary vein divergence from the midvein over the length of the lamina and the angle at which the loop-forming secondaries join the superadjacent secondary (approximately right-angled in Morphotype 5 (Figure 5.6a), obtuse in Morphotype 10).

Discussion

Leaves with entire margins, pinnate camptodromous brochidodromous venation and random reticulate tertiary veins occur within the Magnoliidae (e.g. Magnoliales, Lactoridaceae, Calycanthaceae, Idiospermaceae, Illiciaceae), Hamamelidae (e.g. Balanopales), Caryophyllidae, and Dilleniidae (e.g. Theaceae, Thymelaeales) (Hickey and Wolfe 1975). These types of leaves lack diagnostic features and similar forms are frequently referred simply to *Dicotylophyllum* (Zastawniak 1994) or *Phyllites* (Dusén 1908) in Antarctic leaf floras.

Dutra *et al.* (1998) recorded leaves with features characteristic of the Magnoliidae, Dilleniidae or Rosidae from the Campanian of Nelson Island, South Shetland Islands, but the photographs are too poor to allow comparison. Dusén (1908) illustrated leaves of a similar shape from the Tertiary of the Seymour Island as *Phyllites* sp. 25 but no other features of these Tertiary leaves can be observed.
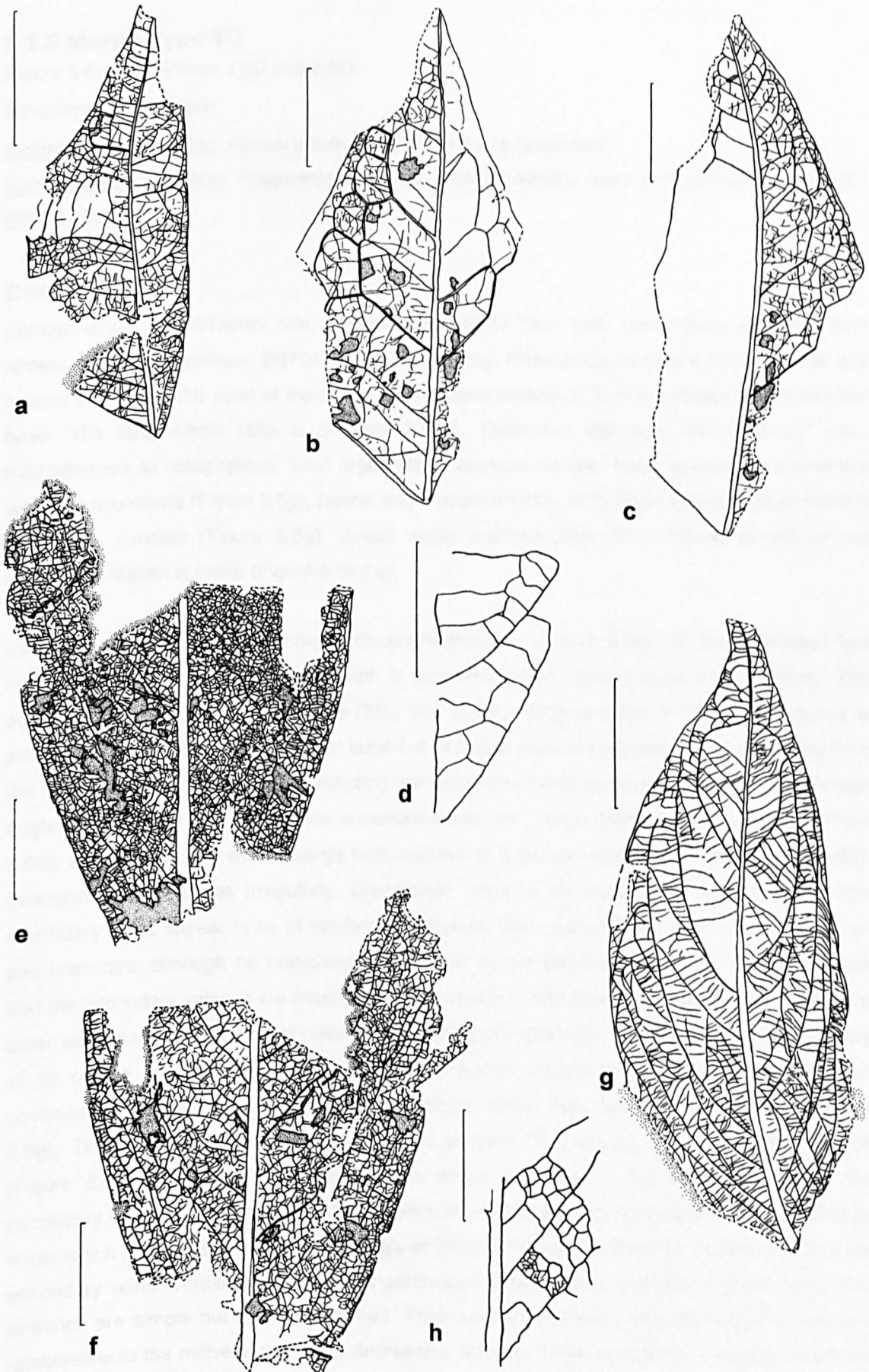
Figure 5.6 Morphotype 5. (a) DJ147.10a. (b) DJ147.32a. (c) DJ147.32a. (d) D8754.8.7a.
Morphotype 5B. (e) D8610.1Aa. (f) D8610.1Ba. (g) D8754.8.41a. (h) D8610.1Aa.
Scale bar is 10mm.

5.2.6 Morphotype 5B

Figure 5.6e,f,g,h. Plates 3.6C and 3.6D.

Specimen numbers

Hidden Lake Formation: Almost whole leaf: D8754.8.41a (excellent).

Santa Marta Formation: Fragmentary leaves: D8610.1Aa&Ba (part and counterpart) (good), D8605.26a (fair).

Description

Lamina length 23.3-51.8mm min. Lamina width 16-37.1mm min. Using measurements from almost complete specimen, D8754.8.41a (Figure 5.6g, Plate 3.6D), lamina is asymmetrical and narrow ovate, with the point of maximum width approximately 32% of the distance from the leaf base. The length/width ratio is at least 2.61:1. Estimated leaf area 445-2395mm^2 min., microphyllous to notophyllous. Leaf organisation appears simple. Apex appears asymmetrical and long acuminate (Figure 5.6g), (apical angle approximately 51°). Base appears asymmetrical and acute cuneate (Figure 5.6g), (basal angle approximately 70°). Petiole absent or not preserved. Margin is entire (Figure 5.6e,f,g).

Venation is pinnate camptodromous eucamptodromous (Figure 5.6g). At the estimated leaf midpoint, the average primary vein width is approximately 0.78mm (range 0.38-1.03mm). The average size is 3.71% (range 2.19-5.75%) and is stout (Figure 5.6g). Primary vein course is either straight or curved. There are at least 5-8 alternate pairs of secondary veins diverging from the midvein at angles of 32-65°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is narrow acute (44°, range 38-48°) (Figure 5.6e,f,g, Plate 3.6C). Basal secondary veins diverge from midvein at a narrow acute angle (40°) (Figure 5.6g). Divergence angle varies irregularly. Divergence angle is symmetrical or asymmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is curved and branched, although no branching is observed in the fragmentary leaves. It also appears that the secondary veins in the most complete specimen, D8754.8.41a (Figure 5.6g), may have outer secondaries but this is not clear. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 114°). The secondaries do appear to join the superadjacent secondaries but they appear to gradually diminish rather than form prominent loops (Figure 5.6g). There are simple intersecondary veins present. The tertiary vein combination is RR (Figure 5.6e,f,g,h). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average angle which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. Tertiary vein pattern is percurrent (Figure 5.6e,f,g,h). Many of the percurrent tertiaries are simple but some are forked. Their course is sinuous and they show an oblique relationship to the midvein, the angle decreasing apically. Their arrangement appears alternate and opposite in about equal proportions and they are closely spaced, with approximately 4-5 veins/cm. Higher order venation is distinct and quaternaries and quinternaries appear relatively randomly oriented (Figure 5.6h). Marginal ultimate venation is looped (Figure 5.6e,f).

Quaternary areolation is imperfect, randomly oriented, irregularly shaped and large (1.3-1.7mm).

Differential characters

This morphotype is distinguished from others within these floras by the possession of pinnate camptodromous eucamptodromous venation (Figure 5.6g, Plate 3.6D). It is differentiated from other morphotypes with a similar venation type by the presence of an entire margin, stout primary (Figure 5.6g) and the approximately right-angled origin of the tertiary veins on the admedial side of the secondaries and on the midvein (Figure 5.6h).

Discussion

Leaves with entire margins and eucamptodromous venation occur within the Magnoliales, several orders of the Dilleniidae and the Anacardiaceae of the Rosidae (Hickey and Wolfe 1975). However, Morphotype 5B shows closest similarity with the Lauraceae, and in particular many species of *Cryptocarya*, *Litsea*, and *Nectandra*. For example, modern species of *Cryptocarya* such as *Cryptocarya melanocarpa* and *Cryptocarya nitens* are strikingly similar to Morphotype 5B. The extant leaves have a similar form, long acuminate apex, acute cuneate base and entire margin. They also share features of venation with Morphotype 5B. The extant leaves possess eucamptodromous venation with 5 or 6 alternate pairs of secondary veins diverging from the midvein at a narrow acute angle, with basal secondaries also narrow acute. The tertiary vein combination is RR and the pattern is percurrent, closely spaced and shows an oblique relationship to the midvein, the angle decreasing apically. The features of the higher order and marginal ultimate venation are also similar in the modern and Cretaceous leaves.

Morphotype 5B is similar to a fragmentary leaf from a laurophyllous plant illustrated by Birkenmajer and Zastawniak (1989a) and described by Zastawniak (1994) from the Santonian-Maastrichtian of King George Island. This leaf was named *Dicotylophyllum* sp. 2 and appears to share several features with Morphotype 5B but it is difficult to compare the two in detail because of the poor preservation of the King George Island leaves. Similarities include an entire margin, camptodromous venation, a stout primary vein, alternate pairs of secondary veins diverging from the midvein at a narrow acute angle and a percurrent tertiary venation pattern. Dusén (1908) also illustrated a fragment from a base of a leaf from the Tertiary of Seymour Island with a similar shape, entire margin and venation and named it *Lauriphyllum nordenskjöldii*. This leaf form was considered to show similarities to the Lauraceae but the poor preservation prevents any further comparison. Orlando (1964) recorded an occurrence of *Nectandra prolifica* from the Tertiary of King George Island, but no comparison is possible because the material was not described or illustrated. The leaves described by Berry (1938) from the Tertiary of Argentina as *Nectandra prolifica* are similar to Morphotype 5B, with an ovate form, acuminate apex, acute cuneate base, entire margin, eucamptodromous venation, and secondary and tertiary veins showing a similar pattern and divergence angles to Morphotype 5B. Berry (1938) was confident of his assignment to the Lauraceae, but doubted assignment to *Nectandra*. Hill (1986)

described lauraceous leaves from the Eocene of New South Wales, such as *Laurophyllum conspicuum,* which shows similar architectural features to Morphotype 5B, including an ovate form and entire margin with eucamptodromous venation, narrow to moderate acute secondary veins and percurrent tertiary veins. Hill (1986) stated that the venation pattern of *L. conspicuum* is common in extant Lauraceae, but he advocated the use of cuticular anatomy in the recognition of Lauraceae.

Based on similarities observed with modern and fossil material, it is concluded that Morphotype 5B may show close affinities to the Lauraceae. The presence of lauraceous leaves on the Late Cretaceous Antarctic Peninsula is supported by the presence of lauraceous wood in the Santonian-Maastrichtian, although these are considered to show closest similarity to *Sassafras* (Poole *et al.,* in press b). Cuticle records (Askin 1992) also provide support for the existence of Lauraceae on the Antarctic Peninsula during the Cretaceous.

5.2.7 Morphotype 6
Figure 5.7a,b,c,d.
Specimen numbers
Hidden Lake Formation: Fragmentary leaves: D8754.8.46d (good), D8754.8.50a (fair), D8754.8.98d (fairly poor).
Santa Marta Formation: Almost whole leaf: D8606.5a (good). Fragmentary leaves: DJ452.2a (good), DJ147.51a (fairly good), DJ147.59a (fairly good), D8606.6a (fair).

Description

Lamina length 12.3-38.1mm min. Lamina width 5.5-25.2mm min. Using measurements from most complete specimens, lamina is asymmetrical and appears to be elliptic to narrow ovate (Figure 5.7b). The length/width ratio is at least 2.65:1. Estimated leaf area 54-1122mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex is not preserved. Base is roughly symmetrical or asymmetrical. Average basal angle is approximately 47° and base is acute and cuneate (Figure 5.7c) to decurrent (Figure 5.7b). A curved normal petiole is present (Figure 5.7b,c), approximately 0.4-2.7mm wide and 3.4-15.2mm long. In DJ452.2a (Figure 5.7d) petiole appears to be winged. Margin is unclear. Best preserved specimens show that the margin is toothed (Figure 5.7a), indented 0.5-1.9mm, average 1mm, 22% of distance to midvein. Teeth are simple and appear to be dentate with acuminate apices (52-76°, average 64°). Sinuses are angular. Margin is too incomplete for quantitative tooth spacing determination. Basal margin is smooth (Figure 5.7b).

Venation appears to be pinnate simple craspedodromous (Figure 5.7a) but the specimens are too fragmentary for the venation type to be confidently categorised. At the estimated leaf midpoint, the average primary vein width is approximately 0.97mm wide (range 0.29-2.05mm). The average size is 9.6% (range 4.48-22.93%) and is massive (Figure 5.7a,b). Since the leaf apex is not preserved in any of the specimens, many of these measurements are maximum

estimates, made closer to the base than the actual leaf midpoint. However, in the most complete leaves, the primary vein is still clearly massive, so this is considered a good definition of primary vein size. Primary vein course appears to be straight and unbranched. There are at least eight subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 6-100°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is narrow acute (43°, range 11-74°) (Figure 5.7a). Basal secondary veins diverge from midvein at a narrow to wide acute angle (8-66°, average 41°). Divergence angle appears to vary irregularly. In the fragmentary specimens, DJ452.2a (Figure 5.7d) and DJ147.59a (Appendix Volume 2 p319), the divergence angle appears to be symmetrical, but in the more complete specimens the secondary vein divergence is more acute on one side of the leaf than the other. The secondary veins appear relatively fine to moderate. In D8606.6a (Appendix Volume 2 p234) the course of the secondary veins is described as curved. However, in the majority of the specimens the course of the secondary veins is recurved or sinuous and branched, although no branching is observed in D8754.8.50a (Figure 5.7c), DJ147.59a (Appendix Volume 2 p319) and D8606.6a (Appendix Volume 2 p234). There are no loop-forming branches. There appears to be intersecondary veins present in some of the specimens and these may be simple, but they are not clear (Figure 5.7a). The tertiary vein combination is RA. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is similar to the average angle of tertiary divergence from the exmedial side of the secondary veins. The leaves are too poorly preserved for the course of the tertiary and higher order veins to be determined.

Differential characters

This morphotype is distinguished from other leaves within the floras by the possession of pinnate simple craspedodromous venation (Figure 5.7a) with a petiolate base (Figure 5.7b), massive primary vein and narrow acute angle of secondary divergence from the midvein (Figure 5.7a). This leaf type is very similar to another fragmentary leaf morphotype, Morphotype 27, but is discriminated from it by the different angles of origin of the tertiary veins. The tertiary vein combination is RA in Morphotype 6 (Figure 5.7d), while it is AR in Morphotype 27.

Discussion

These leaves have features characteristic of the Hamamelidae, Dilleniidae or Rosidae (Hickey and Wolfe 1975), but although these leaves clearly form a separate morphotype, they are too fragmentary for any close comparison with living or fossil leaves.
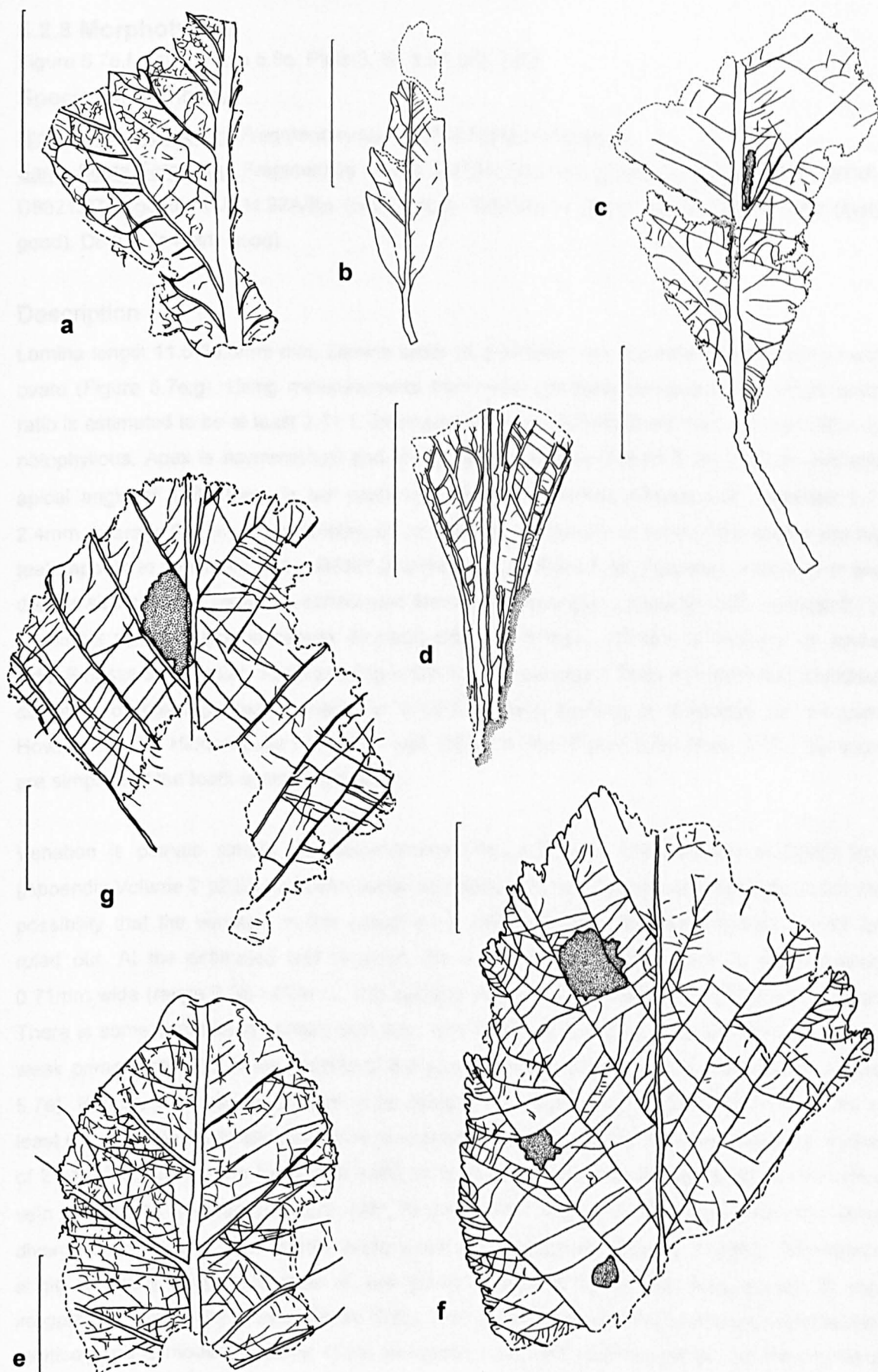
Figure 5.7 Morphotype 6. (a) DJ147.51a. (b) D8606.5a. (c) D8754.8.50a. (d) DJ452.2a.
Morphotype 7. (e) DJ134.13a. (f) D8621.27a. (g) D8616.128a.
Scale bar is 10mm.

5.2.8 Morphotype 7

Figure 5.7e,f,g and Figure 5.8a. Plate 3.7B, 3.8A and 3.8D.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.34a (fairly good).

Santa Marta Formation: Fragmentary leaves: DJ134.13a (fairly good), DJ147.35a (fairly good), D8621.27a (good), DJ134.22A/Ba (fairly good), D8605.31a (fairly good), D8616.128a (fairly good), D8605.7a (fairly good).

Description

Lamina length 11.5-66.6mm min. Lamina width 16.5-59.5mm min. Lamina is asymmetrical and ovate (Figure 5.7e,g). Using measurements from most complete specimens, the length/width ratio is estimated to be at least 2.11:1. Estimated leaf area 383-2642mm^2 min., microphyllous to notophyllous. Apex is asymmetrical and emarginate or obtuse (Figure 5.7e), with an average apical angle of 113°. Base is not preserved. Margin is toothed (Figure 5.7f), indented 0.1-2.4mm, average 0.5mm, approximately 5% of distance to midvein. In most of the specimens the teeth appear to be simple, but in D8621.27a (Figure 5.7f, Plate 3.8A) they are compound, in two distinct size classes. Teeth are serrate and average apical angle is acute (8-138°, average 62°). Dominant serration type is convex on basal side and straight, convex, or concave on apical side. Sinuses are angular. Tooth spacing is 0.3-4.2mm, average 1.7mm. For each leaf, standard deviation of spacing measurements is 0.3-0.7mm and spacing is described as irregular. However, in the Hidden Lake Formation leaf, D8754.8.34a (Figure 5.8a, Plate 3.7B), the teeth are simple and the tooth spacing is regular.

Venation is pinnate simple craspedodromous (Figure 5.7e,f). The venation of D8605.31a (Appendix Volume 2 p229) had been coded as pinnate camptodromous reticulodromous but the possibility that the venation in this specimen is pinnate simple craspedodromous cannot be ruled out. At the estimated leaf midpoint, the average primary vein width is approximately 0.71mm wide (range 0.36-1.02mm). The average size is 2.28% (range 1.01-3.6%) and is stout. There is some variation in primary vein size, with D8621.27a (Figure 5.7f) appearing to have a weak primary vein, but in the majority of the specimens the primary vein is clearly stout (Figure 5.7e). Primary vein course appears to be straight and unbranched (Figure 5.7f). There are at least 6-8 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 21-114°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (49°, range 27-68°) (Figure 5.7e). Basal secondary veins diverge from midvein at a narrow acute angle (31°) (Appendix Volume 2 p262). Divergence angle is nearly uniform in most of the leaves (Figure 5.7e,f,g), but does appear to vary irregularly in some specimens (Figure 5.8a), and is symmetrical. The secondary veins appear relatively fine to moderate. Some of the secondary veins are uniformly curved but the course of the secondaries is described as recurved or sinuous. The secondaries are branched, provided with outer secondaries (Figure 5.7f). There are no loop-forming branches. There appears to be simple intersecondary veins present (Figure 5.7e,f,g). The tertiary vein combination is AR.

There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is similar to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is strongly percurrent (Figure 5.7f,g). These percurrent tertiaries are generally simple and sinuous. They show an oblique relationship to the midvein and the angle decreases apically. Their arrangement is predominantly opposite and they are closely spaced, with 4-6 veins/cm. The higher order venation is not clearly preserved. A darkened area in the apical part of some of the teeth indicates that the teeth may be glandular (Figure 5.8a). The principal vein of the tooth is a secondary, with a slightly eccentric direct course. In the leaves showing compound teeth, a secondary vein serves the primary tooth, while outer secondary veins serve the other orders of teeth (Figure 5.7f, see right hand margin). Accessory veins are not visible.

Differential characters

This morphotype is distinguished from other leaves within these floras by the possession of pinnate simple craspedodromous venation (Figure 5.7f,g, Plate 3.8A). It is set apart from other morphotypes with a similar venation pattern by the presence of an emarginate apex (Figure 5.7e) and outer secondary (Figure 5.7f) as well as intersecondary veins (Figure 5.7f,g). It is considered that the apical margins illustrated in Figure 5.7e are a good representation of the apical form and that the lack of any visible narrowing in primary vein width towards the apex is a feature of the preservation. It should be noted that the Hidden Lake Formation leaf (Figure 5.8a, Plate 3.7B) does not fit well within this group and possibly represents a different taxon.

Discussion

The simple craspedodromous venation, toothed margin and percurrent tertiary veins of this leaf form are characteristic of orders in the Hamamelidae such as the Trochodendraceae, Eupteleales, Urticales, Fagales and Betulales, but also occurs within the Dilleniidae (e.g. Dilleniaceae, Saurauiaceae, Aquifoliaceae) and some families of the Rosidae (Hickey and Wolfe 1975). However, the ovate shape (Figure 5.7e) and compound serrations (see margin on right hand side of D8621.27a, Figure 5.7f) are characteristic of Hamamelid families such as the Eupteleaceae, Betulaceae, and Nothofagaceae (Jones 1986). The regularity of the tertiary venation suggests that this morphotype is of the fourth rank. Although the poor preservation of higher order venation means that this cannot be confirmed, this high rank venation is typical of some species of the Fagaceae and Nothofagaceae (Hickey 1977, Jones 1986). The many outer secondary veins in Morphotype 7 are also very characteristic of fagalean leaves such as Betulaceae and Nothofagaceae.

Dutra (1997b) noted that the architecture of Tertiary leaves assigned to *Nothofagus* from King George Island showed similar morphology to the Betulaceae and phylogenetic analyses have supported a strong relationship between the two. Pole (1992) assigned leaves from the Cretaceous of New Zealand with very similar morphology to Morphotype 7 to the Betulaceae. Morphotype 7 is similar to the New Zealand material in that they share compound teeth with angular sinuses and percurrent tertiaries, but the two forms differ in tooth shape, angle of origin

of tertiary veins and leaf apex style. Although the Betulaceae is believed to have originated in Laurasia during the Cretaceous, the migration to the Southern Hemisphere of members of this family only began in the Oligocene (Chen *et al.* 1999), thus making the suggestion that the leaves of Morphotype 7 are betulaceous somewhat tenuous. *Nothofagidites* pollen, on the other hand, has been recorded within the Santa Marta Formation on James Ross Island (Baldoni and Medina 1989, Baldoni 1992, Keating 1992). Hill *et al.* (1996) state that higher order serrations with finer branches ending in serrations of a size which correlates to the size of the respective vein is a common feature of extant deciduous *Nothofagus* leaves. This feature is observed in these specimens. Morphotype 7 has very similar features to extant deciduous species such as *N. glauca* from South America, with secondary veins ending in major serrations and large numbers of minor serrations fed by outer secondary veins (Tanai 1986, Hill *et al.* 1996).

Cantrill and Nichols (1996) erected the form genus *Gnafalea* (an anagram of fagalean) for poorly preserved pinnately veined leaves from the Southern Hemisphere and recorded two species from the late Albian of Alexander Island. Morphotype 7 is very similar to one of these, *G. jeffersonii*, which has a similar size, form, venation pattern, compound tooth series, and possible presence of outer secondary veins. However, *G. jeffersonii* has a dentate rather than a serrate margin. In addition, absence of any preserved tertiary venation prevents further comparison. Cantrill and Nichols (1996) suggested that this leaf form showed affinities to 'higher' Hamamelidae or lower pinnate Dilleniidae, but without tertiary vein preservation, could not make any further determination. Morphotype 7, however, conforms to the criteria quoted by Scriven *et al.* (1995) from Pole (1993b,c, 1994) for the recognition of *Nothofagus,* with regularly spaced secondary veins, outer secondaries, simple craspedodromous venation, percurrent tertiaries, a toothed margin, an ovate form, and an association with *Nothofagus* pollen. Dutra (1997b) recorded several species of primitive leaves of the Nothofagaceae from the late Campanian to Eocene of King George Island. The Santa Marta Formation (Santonian-?early Campanian) leaves of Morphotype 7 show similarities to the Campanian *Nothofagus* leaf form, *Nothofagus cretacea,* but the King George Island leaves have no outer secondaries visible. This difference, however, may simply be due to the poorer preservation of the King George Island specimens. The leaves of *N. cretacea* described by Zastawniak (1990, 1994) from the Santonian-Maastrichtian of King George Island are also poorly preserved with no margins, but do have a similar size and form to Morphotype 7. Morphotype 7 and *N. cretacea* also share the regular and roughly parallel secondary veins with slightly curved outer secondaries characteristic of *Nothofagus. Nothofagus subferruginea* reported from the Campanian-Tertiary of King George Island (Zastawniak 1981, Czajkowski and Rösler 1986, Birkenmajer and Zastawniak 1989a, Dutra 1989, Li 1994) and Seymour Island (formerly *Fagus obscura*) (Dusén 1908) is different to Morphotype 7 because the teeth of *N. subferruginea* are mostly simple (Tanai 1986).

One of the most similar fossil species to Morphotype 7 is *Nothofagus variabilis* reported from the Miocene of Argentina (Tanai 1986), with a similar shape, venation pattern and marginal features. It, too, has double serrations with large teeth and an angular sinus, the principal teeth

pointed with small subsidiary teeth on the apical side and basal side. There are differences, though, such as the shape of the leaf apex. However, *N. variabilis* has also been illustrated from the Oligocene-Miocene of King George Island (Zastawniak *et al.* 1985, Birkenmajer and Zastawniak 1989) and, although the lack of a description for the King George Island material prohibits detailed comparison, the photograph shows that this leaf form possesses an obtuse apex, similar to Morphotype 7. Li (1994) also described nothofagaceous leaves from the Eocene of King George Island and called them *Nothofagus oligophlebia*, stating that this species is very similar to *N. variabilis* from Argentina. *N. oligophlebia* and Morphotype 7 are similar in that *N. oligophlebia* possesses compound teeth, but the teeth are a different shape and are described as spinose. The King George Island leaves also differ from Morphotype 7 in shape, apical and basal style, and secondary and tertiary vein pattern and therefore may not be put into the same taxon.

Leaves similar to those of *Nothofagus* have also been reported by Jefferson (1980), Thomson and Burn (1977) and Dusén (1908) from the Late Cretaceous to Tertiary of Adelaide Island, Alexander Island, and Seymour Island, respectively, but are too poorly preserved to warrant further comparison. There have been numerous reports of wood (e.g. Francis 1986, 1991, 1999) and pollen (e.g. Stuchlik 1981, Dettmann and Thomson 1987, Baldoni and Medina 1989, Baldoni 1992, Keating 1992) assigned to the Nothofagaceae from the Santonian onwards in the South Shetland Islands and the James Ross Basin.

5.2.9 Morphotype 8
Figure 5.8b,c,d,e. Plate 3.11C.

Specimen numbers

<u>Hidden Lake Formation</u>: Fragmentary leaves: D8754.8.60a (good), D8754.8.8b (fairly good), D8754.8.54b (fair), D8754.8.60b (poor).

<u>Santa Marta Formation</u>: Fragmentary leaves: D8605.27Aa&Ba (part and counterpart) (fairly good), DJ147.4a (fair), DJ147.30a (fairly good), DJ147.34a (fairly good).

Description

Lamina length 15.3-53.3mm min. Lamina width 11.1-46mm min. Specimens are too fragmentary for lamina symmetry or form to be confidently described. The length/width ratio is estimated to be at least 1.16:1. Estimated leaf area 113-1635mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex not preserved. Average basal angle is estimated to be approximately 96° and base is obtuse (normal or cuneate) (Figure 5.8b, Plate 3.11C) or acute decurrent (Figure 5.8c). Petiole absent or not preserved. Margin is toothed (Figure 5.8b,e), indented 0.1-1.8mm, average 0.5mm, approximately 4% of distance to midvein. Teeth are simple, serrate and average apical angle is acute to obtuse (21-152°, average 73°). Dominant serration type is convex on basal side and straight on apical side. Sinuses are quite rounded. Tooth spacing is 0.4-7.6mm, average 3.3mm. For each leaf, standard deviation of spacing measurements is 0.3-1.1mm and in the best preserved specimens spacing is regular.

Venation is suprabasal acrodromous (Figure 5.8b,c, Plate 3.11C). The leaves are incomplete but from the parts present it is assumed that there are two strongly developed secondary veins arising 3-4mm above the leaf base and running in convergent arches toward the leaf apex. The development appears to be perfect, but since the apical part of the leaf is missing the development cannot be confidently described. At the estimated leaf midpoint, the average primary vein width is approximately 0.52mm (range 0.22-0.98mm). The average size is 1.59% (range 1.05-2.25%) and is moderate. Primary vein course is straight (Figure 5.8b). The acrodromous secondary veins diverge from the midvein at a narrow acute angle (38-40°, average 39°) (Figure 5.8b). There is only one prominent acrodromous secondary vein and in all the specimens only one side of the leaf is preserved so symmetry cannot be assessed. These secondary veins are moderate to relatively thick. Their course is described as uniformly curved and unbranched. The tertiary vein combination is AR (Figure 5.8b). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an acute angle, with an average which is approximately equal to the average angle of tertiary divergence from the exmedial side of the secondary veins. Tertiary venation pattern is weakly percurrent (Figure 5.8b). Percurrent tertiaries are forked and recurved and their relationship to the midvein is approximately right-angled. Their arrangement is predominantly alternate and they are closely spaced with approximately 5 veins/cm. On the exmedial side of the acrodromous vein the tertiary veins form loops (Figure 5.8b). Higher vein orders are distinct. Quaternary and quinternary veins are orthogonal (Figure 5.8d). Marginal ultimate venation is looped (Figure 5.8b,e). Quaternary areolation appears imperfect, randomly arranged, irregularly shaped and large to very large (1.5-2.5mm). There is no evidence of darker material, which may have indicated glands, in the tooth apices, and apices appear simple. Principal vein of the tooth is a tertiary with a central deflected course. Accessory veins appear incomplete or looped (Figure 5.8e). The vein organisation is of the third rank with tertiaries having relatively consistent courses, but areoles of irregular size and orientation.

Differential characters

These leaves are distinguished from other morphotypes in this study because they are the only morphotype with acrodromous venation in combination with a toothed margin (Figure 5.8b,e, Plate 3.11C). They can also be distinguished from the other leaves with acrodromous venation by the size of the primary vein and the acute angle of origin of tertiary veins on the midvein.

Discussion

The combination of acrodromous venation and a toothed margin is found within the Laurales (Amborellaceae, Hernandiaceae, and some Lauraceae) and also the Urticaceae and Ulmaceae of the Urticales (Hickey and Wolfe 1975). Although well preserved, the teeth of Morphotype 8 show insufficient detail to facilitate differentiation between these two major groups. No similar modern lauralean leaves could be found, but using the computerised identification key for Australian tropical rain forest trees (Hyland and Whiffin 1993) a very similar leaf form to Morphotype 8 was found. *Celtis timorensis* of the Ulmaceae has a similar shaped leaf base and teeth, with acrodromous veins diverging at a narrow acute angle to the midvein, a straight

midvein, and a tertiary vein combination of AR. The tertiary venation pattern appears very similar, with weakly percurrent tertiaries showing an approximately right-angled relationship to the midvein with looping tertiaries on the exmedial side of the acrodromous veins. A branch from the outside of these tertiary loops enters the teeth and the quaternary venation also appears to be orthogonal. These features are all shared with Morphotype 8, but since all the Cretaceous leaves of this group are fragmentary, it is not possible to confidently assign these specimens to this genus or family. In addition, there are no other records of this family in the Antarctic Peninsula and there are no Cretaceous fossil leaves showing similar architecture to these James Ross Island specimens. Berry (1938) described leaves from the Tertiary of Argentina as *Celtis ameghinoi*, but these leaves were not illustrated, prohibiting comparison with Morphotype 8.

5.2.10 Morphotype 9

Figure 5.8f,g. Plate 3.7E.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.16b (good).

Description

Lamina length 12.9mm min. Lamina width 15.4mm min. The leaf appears to be oblate to orbiculate (Figure 5.8f, Plate 3.7E) but the leaf is too incomplete for lamina form or symmetry to be confidently described. The length/width ratio is at least 0.84:1. Estimated leaf area 130mm² min., microphyllous. Leaf organisation appears simple. Apex not preserved. Base is rounded with an estimated basal angle of approximately 133° (Figure 5.8f). A curved petiole, approximately 1.2mm wide and 3.4mm long, is present and appears winged (Figure 5.8f). Margin is entire (Figure 5.8f).

Venation is basal acrodromous, with two strongly developed secondary veins running in convergent arches toward the leaf apex (Figure 5.8f,g, Plate 3.7E). The development appears to be perfect but since the leaf apex is incomplete this is not certain. The primary vein tapers from 0.7mm near the base to 0.3mm in the apical part of the leaf. At the estimated leaf midpoint, the primary vein width is approximately 0.33mm. The size is 2.18% and is stout. Primary vein course is straight (Figure 5.8f). There is one pair of opposite secondary veins. These acrodromous secondary veins diverge from the midvein at a wide acute angle (58-75°, average 66°). The divergence angle is more acute on one side of the leaf than the other. These secondary veins are relatively thick, approximately 0.1-0.5mm wide. Their course is curved and unbranched. The tertiary vein combination is RR (Figure 5.8f,g). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. On the admedial side of the acrodromous secondaries, the pattern formed by the tertiaries is weakly percurrent (Figure 5.8f,g). The percurrent tertiaries are forked, recurved, and their relationship to the midvein is

approximately right-angled. Their arrangement is predominantly alternate and they are closely spaced, with approximately 8 veins/cm. On the exmedial side of the secondaries the tertiaries form loops. The higher order venation is not well preserved, but quaternaries appear orthogonal and marginal ultimate venation is looped (Figure 5.8f,g). Quaternary areolation appears imperfect, randomly arranged, irregularly shaped and medium sized (0.4-0.7mm).

Differential characters

This leaf is separated from most other morphotypes in this study by the possession of acrodromous venation in association with a smooth margin (Figure 5.8f,g, Plate 3.7E). Leaves of Morphotype 11 also have these characters but differ from Morphotype 9 because Morphotype 9 has a rounded petiolate base, a stout midvein, a wide acute angle of divergence of the basal acrodromous secondary veins, and approximately right-angled origin of tertiary veins on the exmedial side of the acrodromous secondary veins.

Discussion

Leaves with acrodromous venation and entire margins with percurrent tertiary veins are characteristic of the Piperales, Aristolochiales, and Laurales (Amborellaceae, Hernandiaceae, and some Lauraceae) (Hickey and Wolfe 1975). Leaves with a very similar shape and venation to Morphotype 9 are found within the Lauraceae, e.g. species of *Cinnamomum*. Similarities with this species include the rounded petiolate base, entire margin, single pair of basal perfect acrodromous secondary veins, weakly percurrent tertiaries showing an approximately right-angled relationship to the midvein, looping tertiaries on the exmedial side of the acrodromous veins and orthogonal quaternaries. The principal difference is the angle of divergence of the acrodromous veins, which is more obtuse in Morphotype 9 than observed within *Cinnamomum*.

Cantrill and Nichols (1996) described a lauralean leaf form, *Timothyia trinervis*, from the late Albian of Alexander Island. This leaf is a similar shape and size with a rounded petiolate base, an entire margin, and acrodromous venation, but the acrodromous veins are acute decurrent on the midvein in *T. trinervis*. One of the leaves illustrated under Form D cf. *Cinnamomoides* of Rees and Smellie (1989) from the Cenomanian-Campanian of Williams Point, Livingston Island, has a similar form, size, entire margin and perfect acrodromous venation, but the position of the acrodromous venation is suprabasal. Dusén (1908) also illustrated a leaf, *Phyllites* sp. 3, with a rounded base, entire margin and suprabasal acrodromous venation, from the Tertiary of Seymour Island. However, the most similar fossil is Lauraceae sp. A, described by Pole (1993a) from the early Miocene of New Zealand. This leaf form has a rounded petiolate base, an entire margin, basal perfect acrodromous venation, weakly percurrent tertiaries with an approximately right-angled relationship to the midvein, a tertiary combination of RR, and looping tertiaries on the exmedial side of the acrodromous veins. Morphotype 9 does, therefore, appear to show affinities with the Lauraceae, but unfortunately it is only a fragmentary specimen.
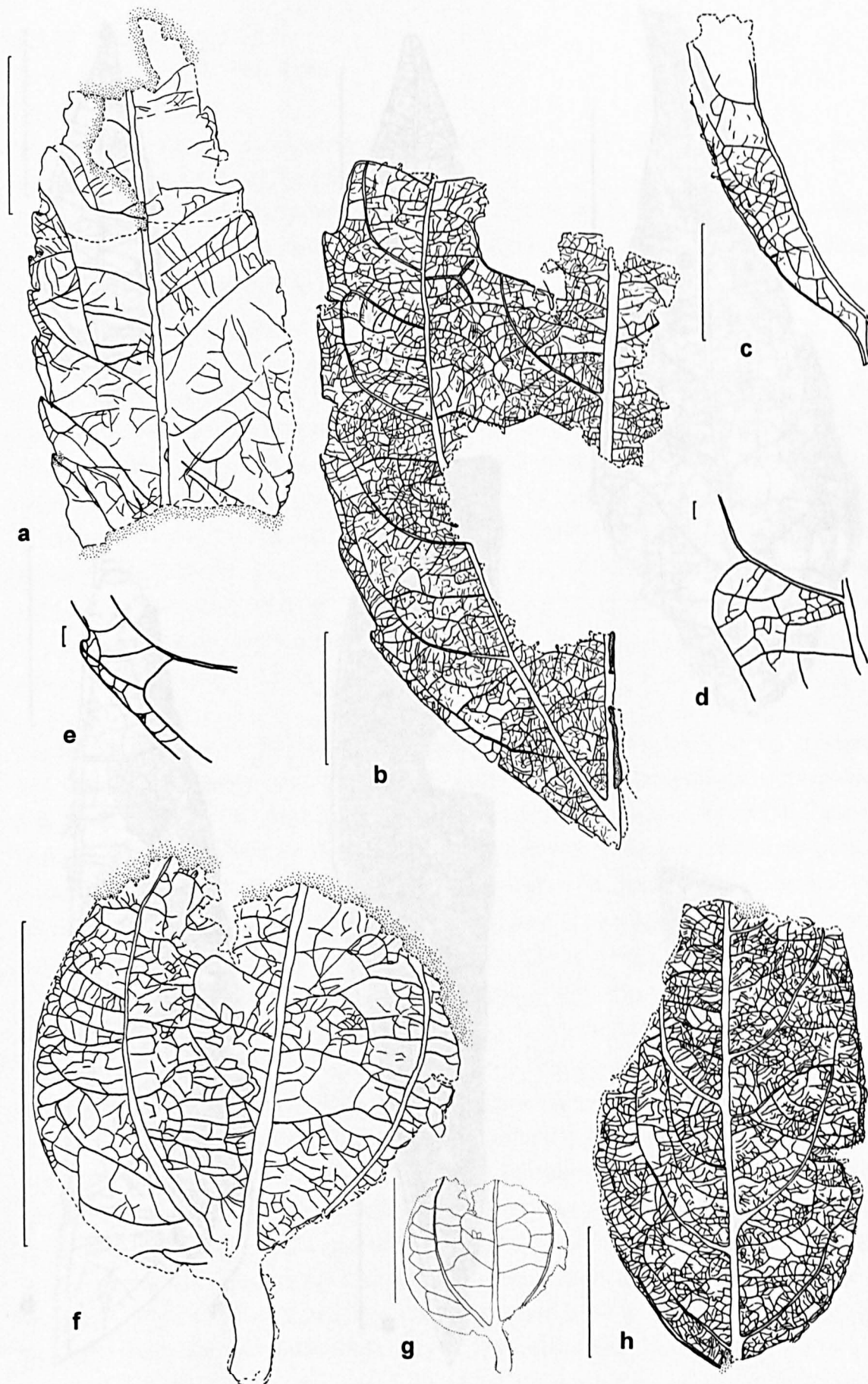
Figure 5.8 Morphotype 7. (a) D8754.8.34a. Morphotype 8. (b) D8754.8.60a. (c) DJ147.4a.
(d) D8754.8.60a. (e) D8754.8.60a. Morphotype 9. (f) D8754.8.16b.
(g) Simplified drawing of D8754.8.16b. Morphotype 10. (h) D8754.8.42a.
Scale bar is 10mm in (a), (b), (c), (f), (g) and (h). Scale bar is 1mm in (d) and (e).
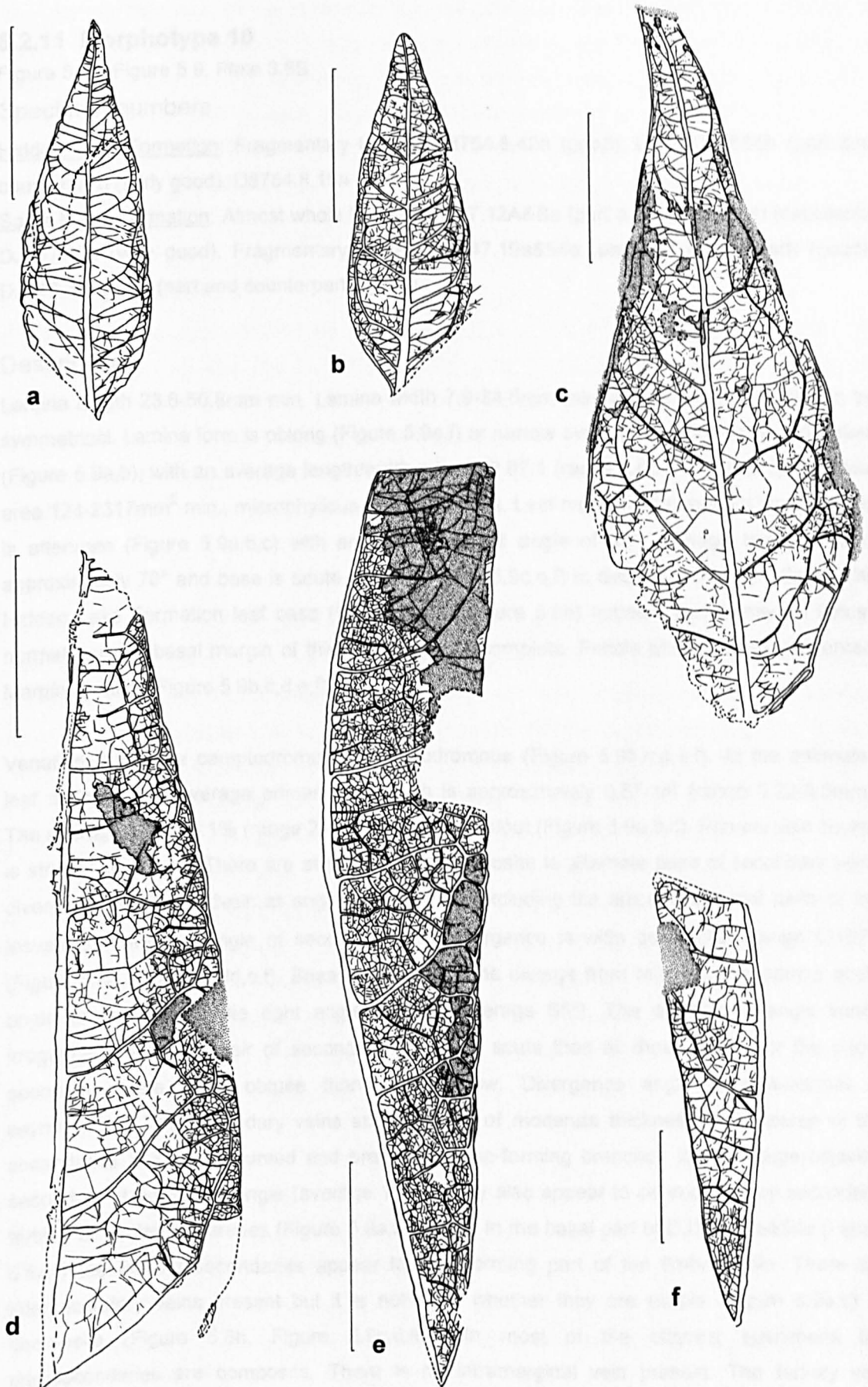
**Figure 5.9 Morphotype 10. (a) DJ147.12Aa. (b) DJ147.12Ba. (c) DJ147.46a.
(d) DJ147.38Aa. (e) DJ147.19a. (f) DJ147.54a.
Scale bar is 10mm.**

5.2.11 Morphotype 10

Figure 5.8h, Figure 5.9. Plate 3.8B.

Specimen numbers

Hidden Lake Formation: Fragmentary leaves: D8754.8.42a (good), D8754.8.4b&5b (part and counterpart) (fairly good), D8754.8.15a (fair).

Santa Marta Formation: Almost whole leaves: DJ147.12A&Ba (part and counterpart) (excellent), DJ147.46a (very good). Fragmentary leaves: DJ147.19a&54a (part and counterpart) (good), DJ147.38Aa&Ba (part and counterpart) (good).

Description

Lamina length 23.6-50.8mm min. Lamina width 7.9-34.8mm min. Whole lamina appears to be symmetrical. Lamina form is oblong (Figure 5.9e,f) or narrow ovate (Figure 5.9c,d) to lanceolate (Figure 5.9a,b), with an average length/width ratio of 2.87:1 (range 2.68-3.01:1). Estimated leaf area 124-2317mm^2 min., microphyllous to notophyllous. Leaf organisation appears simple. Apex is attenuate (Figure 5.9a,b,c) with an average apical angle of 34°. Average basal angle is approximately 70° and base is acute normal (Figure 5.9c,e,f) to decurrent (Figure 5.9a,b). The Hidden Lake Formation leaf base (D8754.8.42a, Figure 5.8h) appears that it may be obtuse normal, but the basal margin of this specimen is incomplete. Petiole absent or not preserved. Margin is entire (Figure 5.9b,c,d,e,f).

Venation is pinnate camptodromous brochidodromous (Figure 5.9b,c,d,e,f). At the estimated leaf midpoint, the average primary vein width is approximately 0.57mm (range 0.22-0.8mm). The average size is 3.1% (range 2.46-3.61%) and is stout (Figure 5.9a,b,c). Primary vein course is straight or curved. There are at least 6-12 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 34-113°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is wide acute (72°, range 61-87°) (Figure 5.8h, Figure 5.9d,e,f). Basal secondary veins diverge from midvein at a narrow acute angle to an approximate right angle (36-98°, average 65°). The divergence angle varies irregularly, the lowest pair of secondaries is more acute than all those above, or the upper secondaries are more obtuse than those below. Divergence angle is symmetrical or asymmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 110°). They also appear to be enclosed by secondary, tertiary or quaternary arches (Figure 5.9a,b,c,d,e,f). In the basal part of DJ147.19a&54a (Figure 5.9e,f) the looping secondaries appear to fuse forming part of the fimbrial vein. There are intersecondary veins present but it is not clear whether they are simple (Figure 5.9a,b) or composite (Figure 5.8h, Figure 5.9c,d,e,f). In most of the clearest specimens the intersecondaries are composite. There is no intramarginal vein present. The tertiary vein combination is RR (Figure 5.8h, Figure 5.9c,d,e,f). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is approximately equal to the average angle of tertiary divergence

from the exmedial side of the secondary veins (Figure 5.8h, Figure 5.9e,f). The tertiary vein pattern is random reticulate to weakly percurrent (Figure 5.9e). The higher vein orders are distinct. The quaternary and quinternary veins are relatively randomly oriented (Figure 5.9e). There is a fimbrial vein present (Figure 5.9d,e). The veinlets appear to be branched. The areolation formed by the quaternary veins appears to be imperfect with a random arrangement. The shape of the areoles is irregular and they appear to be medium-sized (approximately 0.5-1mm).

Differential characters

Morphotype 10 is characterised by pinnate camptodromous brochidodromous venation, an entire margin and an attenuate apex (Figure 5.9a,b,c,d,e,f) and is very similar to Morphotype 5, as discussed above. However, Morphotype 10 can be distinguished from Morphotype 5 by its acute normal to decurrent basal style, the variation in secondary vein divergence from the midvein over the length of the lamina and the obtuse angle at which the loop-forming secondaries join the superadjacent secondary.

Discussion

Leaves with entire margins, pinnate camptodromous brochidodromous venation and random reticulate tertiary veins occur within the Magnoliidae (e.g. Magnoliales, Laurales, Illiciaceae), Hamamelidae (e.g. Balanopales), Caryophyllidae, and Dilleniidae (e.g. Theaceae, Thymelaeales) (Hickey and Wolfe 1975), but no further determinations were possible because many plant groups display the features observed in Morphotype 10. Berry (1938) described a leaf form with some similar features to Morphotype 10 from the Tertiary of Argentina as *Myristica? fossilis*. The similarities include an oblong form and entire margin with brochidodromous venation and a similar number of secondary veins diverging from the stout midvein at wide acute angle. *M. fossilis* also possesses a rounded base and the loop-forming branches appear to join the superadjacent secondary at an acute angle, so in these respects differs from Morphotype 10. The similarities discussed, however, do not suggest affinities to the Myristicaceae because Berry (1938) did not believe that the Argentine material showed any greater similarity to *Myristica* than to leaves from many unrelated groups. Modern leaves of the Myristicaceae, such as *Myristica insipida*, show weakly percurrent tertiary veins and are thus dissimilar to Morphotype 10.

5.2.12 Morphotype 11

Figure 5.10. Plates 3.6B and 3.9D.

Specimen numbers

Hidden Lake Formation: Almost whole leaf: D8754.8.57a (excellent). Fragmentary leaves: D8754.8.54a (excellent), D8754.8.44a (good).

Santa Marta Formation: Fragmentary leaves: D8605.33a (very good), DJ147.52a (good), DJ134.6a (fair).

Description

Lamina length 14.2-60.3mm min. Lamina width 10.6-21.6mm min. Lamina appears slightly asymmetrical and form is narrow elliptic (Figure 5.10d, Plate 3.6B) to lanceolate (Figure 5.10b, Plate 3.9D), with an average length/width ratio of approximately 3.23:1 (range 2.93-3.52:1). Estimated leaf area 264-1005mm^2 min., microphyllous. Leaf organisation appears simple. Apical margins are not completely preserved but apex appears to be roughly symmetrical and attenuate (Figure 5.10d) to long acuminate (Figure 5.10b) (average apical angle approximately 46°). Leaf base is roughly symmetrical and acute normal (Figure 5.10c) to cuneate (Figure 5.10a,b,d), with an average basal angle of approximately 55°. Petiole absent or not preserved. Margin is entire (Figure 5.10a,b,c).

Venation is acrodromous (Figure 5.10b,d,f, Plate 3.6B), with two strongly developed secondary veins running in convergent arches toward the leaf apex. The position is basal to suprabasal, with the secondary veins arising up to 22.6mm (average 5.3mm) from the leaf base. The development is perfect, with the acrodromous veins reaching the leaf apex or running to at least 69% of the distance to the leaf apex. At the estimated leaf midpoint, the average primary vein width is approximately 0.52mm (range 0.38-0.69mm). The average size is 4.05% (range 2.62-5.56%) and is massive (Figure 5.10b,c). Primary vein course is markedly curved (Figure 5.10b,d), only appearing straight in the fragmentary specimens. There are up to 5-7 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 19-86°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence for each leaf is moderate acute (51°, range 37-63°) (Figure 5.10b,c,d). The acrodromous secondary veins diverge from midvein at a narrow to moderate acute angle (26-50°, average 36°) (Figure 5.10b,d). The acrodromous secondary veins are more acute than all the secondary veins above. In most specimens the secondary vein divergence angle is more acute on one side of the leaf than the other, but in D8754.8.54a (Figure 5.10d) it is symmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is curved and unbranched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 103°) (Figure 5.10d). They also appear to be enclosed by tertiary or quaternary arches (Figure 5.10b). There may be composite intersecondary veins present, but these are not clear (Figure 5.10c). The tertiary vein combination is AR (Figure 5.10a,b,d,f). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is similar to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary vein pattern is weakly percurrent (Figure 5.10a,d,e,f). The percurrent tertiaries appear predominantly simple but some appear forked. Their course is recurved to sinuous. The relationship of the percurrent tertiaries to the midvein is roughly perpendicular to oblique, the angle decreasing apically. The arrangement appears to be alternate and opposite in about equal proportions. The interval between tertiary veins is close, with 4-7 veins/cm. On the exmedial side of the secondary veins the tertiaries form loops, which merge together near the margin. The higher order venation is not clearly preserved but the quaternary veins appear to be randomly oriented to orthogonal (Figure 5.10e) and the marginal ultimate venation appears to be looped (Figure 5.10a). The

quaternary areolation appears to be imperfect to incomplete, but aligned roughly parallel to the midvein and of medium to large size (approximately 0.4-1.2mm).

Differential characters

These leaves are distinguished from the other morphotypes by their combination of acrodromous venation, smooth margin, narrow elliptic to lanceolate form and acute base (Figure 5.10b,d,f, Plate 3.6B). The massive primary vein and presence of numerous secondary veins also distinguishes this morphotype from other leaves with acrodromous venation within the floras (Figure 5.10b, Plate 3.9D).

Discussion

Leaves with acrodromous venation and entire margins with percurrent tertiary veins are characteristic of the Piperales, Aristolochiales, and Laurales (Amborellaceae, Hernandiaceae, and some Lauraceae) (Hickey and Wolfe 1975). The leaf architecture is characteristic of many genera of the Lauraceae, such as *Cinnamomum* and *Neolitsea*, but similar forms also occur within other lauralean families, such as *Hortonia* of the Monimiaceae.

Dutra *et al.* (1998) recorded leaves with cinamophyllic and laurophyllic architecture and a similar shape to Morphotype 11 from the Campanian of Nelson Island, but these leaves are too poorly preserved for further comparison. Dusén (1908) illustrated a leaf form from the Tertiary of Seymour Island named *Lauriphyllum nordenskjoldii*. The part of the leaf preserved is not dissimilar to Morphotype 11, but as stated in the discussion of Morphotype 5B, the fossil of *L. nordenskjoldii* is too fragmentary for detailed comparison with these Cretaceous specimens. The laurophyllous leaves described by Zastawniak (1994) from the Santonian-Maastrichtian of King George Island, discussed under Morphotype 5B, lack the strong acrodromous veins observed in Morphotype 11. Zastawniak (1994) described a leaf with acrodromous venation named *Dicotylophyllum* sp. 5 from the same flora. This leaf specimen is poorly preserved, with the apex, base and leaf margin missing, however, the style of the acrodromous veins present in *Dicotylophyllum* sp. 5 appears more similar to the leaf form named *Pentaneurum dusenii* from Tertiary strata of King George Island by Li (1994) than Morphotype 11. *P. dusenii* was suggested to show affinities to the Melastomataceae and is different to the acrodromous leaf forms under study here because it possesses five acrodromous veins instead of three. Morphotype 11 is most similar to the leaves described as Form D cf. *Cinnamomoides* by Rees and Smellie (1989) from the Cenomanian-Campanian of Williams Point, Livingston Island. These leaves have a similar shape, size, entire margin and suprabasal perfect acrodromous venation.
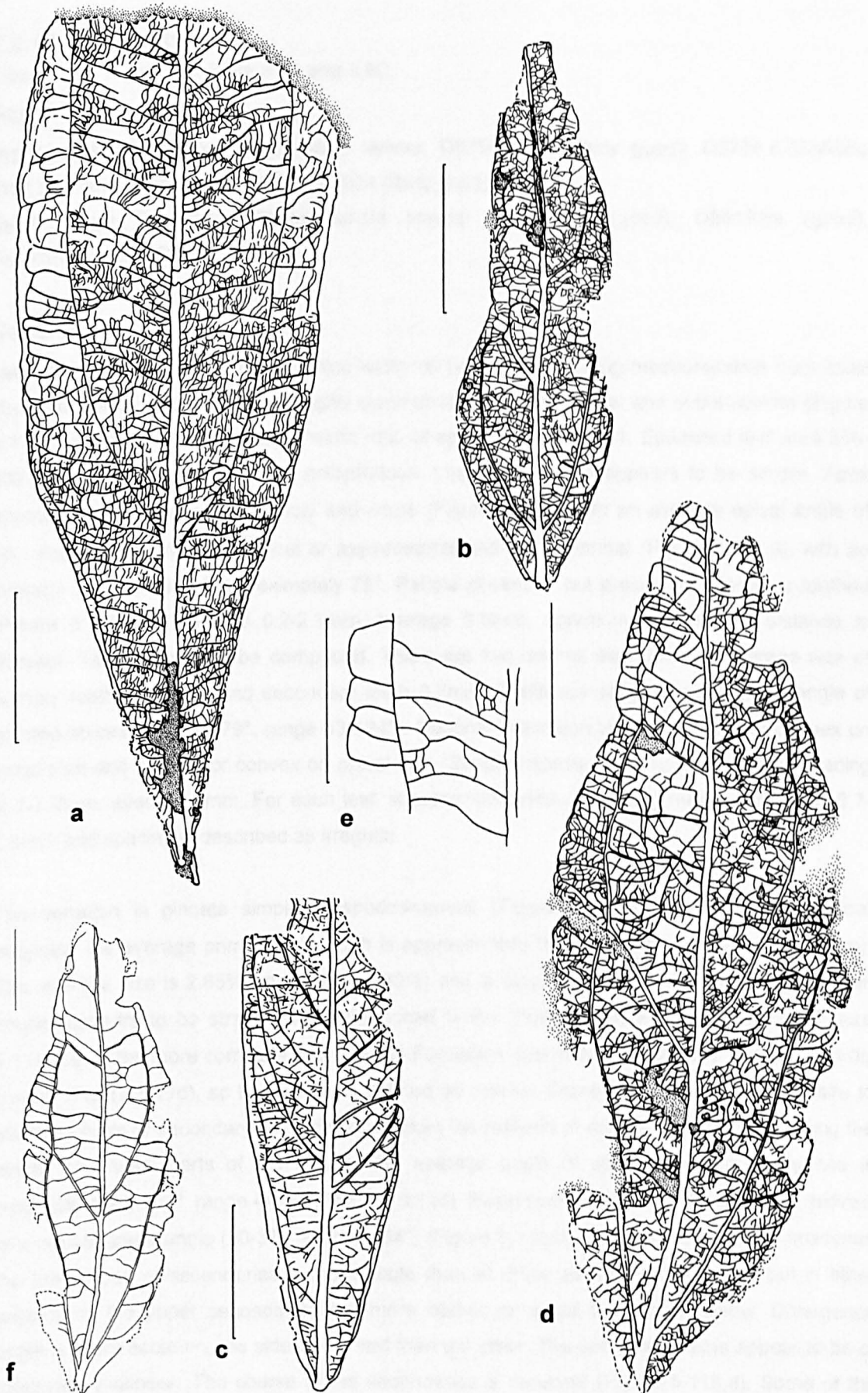
Figure 5.10 Morphotype 11. (a) D8754.8.44a. (b) D8754.8.57a. (c) D8605.33a.
(d) D8754.8.54a. (e) D8754.8.44a. (f) Simplified drawing of D8754.8.54a.
Scale bar is 10mm.

5.2.13 Morphotype 12
Figure 5.11, Figure 2.3. Plate 3.7A and 3.8C.

Specimen numbers

Hidden Lake Formation: Fragmentary leaves: D8754.8.47a (fairly good), D8754.8.32a&98e (part and counterpart) (fair), D8754.8.101a (fairly good).

Santa Marta Formation: Almost whole leaves: D8616.74a (good), D8619.6a (good). Fragmentary leaf: D8606.8a (fair).

Description

Lamina length 21.5-48mm min. Lamina width 16.1-66mm min. Using measurements from most complete specimens, lamina is roughly symmetrical or asymmetrical and suborbiculate (Figure 5.11c,d, Plate 3.7A), with a length/width ratio of approximately 1.49:1. Estimated leaf area 256-4327mm^2 min., microphyllous to notophyllous. Leaf organisation appears to be simple. Apex appears to be roughly symmetrical and acute (Figure 5.11d), with an average apical angle of 75°. Base is roughly symmetrical or asymmetrical and acute normal (Figure 5.11c,d), with an average basal angle of approximately 75°. Petiole absent or not preserved. Margin is toothed (Figure 5.11b,e,f), indented 0.2-2.1mm, average 0.8mm, approximately 10% of distance to midvein. Teeth appear to be compound. There are two distinct size classes; average size of primary teeth is 1.6mm and secondary teeth 0.7mm. Teeth are serrate and average angle of pointed apices is acute (79°, range 43-124°). Dominant serration type is concave or convex on basal side and straight or convex on apical side. Sinuses appear quite rounded. Tooth spacing is 1-7.9mm, average 4mm. For each leaf, standard deviation of spacing measurements is 0.7-2.5mm and spacing is described as irregular.

The venation is pinnate simple craspedodromous (Figure 5.11c,d). At the estimated leaf midpoint, the average primary vein width is approximately 0.75mm wide (range 0.54-0.94mm). The average size is 2.85% (range 2.04-3.89%) and is stout (Figure 5.11c,d). The primary vein course appears to be straight and unbranched in the Hidden Lake Formation leaves (Figure 5.11a) but in the more complete Santa Marta Formation specimens the primary vein is markedly curved (Figure 5.11d), so the course is defined as curved. There are up to 5-9 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 21-90°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (51°, range 44-65°) (Figure 5.11d). Basal secondary veins diverge from midvein at a narrow acute angle (30-37°, average 34°) (Figure 5.11c,d). In the most complete specimen the lowest pair of secondaries is more acute than all those above (Figure 5.11d) but in other specimens the upper secondaries are more obtuse or acute than those below. Divergence angle is more acute on one side of the leaf than the other. The secondary veins appear to be of moderate thickness. The course of the secondaries is recurved (Figure 5.11b,d). Some of the secondary veins in D8619.6a (Figure 5.11c, Plate 3.8C) appear to be sinuous but the surface of this specimen is very uneven. In the specimens with the clearest venation the secondaries are branched and provided with outer secondaries (Figure 5.11b,d, Figure 2.3b), but these are not

visible in all specimens. The tertiary vein combination is AA (Figure 5.11b,f). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an acute angle, with an average which is approximately equal to the average angle of tertiary divergence from the exmedial side of the secondary veins (Figure 5.11d). The tertiary venation pattern is percurrent (Figure 5.11c,f). The percurrent tertiaries are simple or forked and they show an oblique relationship to the midvein, the angle decreasing apically. Their arrangement is alternate and opposite in about equal proportions and they are closely spaced, with approximately 3-5 veins/cm. The higher order venation is not clearly preserved. There is no clear evidence of possible glands in the teeth (Figure 5.11e,f). The primary teeth are served by secondary veins following a central and direct course, with accessory veins that appear to terminate at the tooth apex. Tertiary veins following a deflected course serve the secondary teeth (Figure 5.11b,f).

Differential characters

This morphotype is distinguished from the other morphotypes within these floras by the possession of pinnate simple craspedodromous venation along with an elliptic form and acute normal base (Figure 5.11c,d). It can also be differentiated from other morphotypes such as Morphotype 7 with simple craspedodromous venation by the acute angle of origin of tertiary veins on the midvein (Figure 5.11d) and the nature of the margin (Figure 5.11f). In Morphotype 12 the course of the secondary veins serving the primary teeth is central rather than eccentric as in Morphotype 7. The accessory veins terminating at the tooth apices in Morphotype 12 are not observed in Morphotype 7. In addition, tertiary veins following a deflected course serve the secondary teeth in Morphotype 12, while outer secondary veins serve the secondary teeth in Morphotype 7.

Discussion

Leaves with simple craspedodromous venation and toothed margins occur within the Ranunculidae, Dilleniidae, Rosidae and Hamamelidae (Hickey and Wolfe 1975). The leaves of Morphotype 12 can be placed within the Hamamelidae based on their possession of urticoid teeth. The teeth of Morphotype 12 are considered most similar to the urticoid type because they are a similar shape, non-glandular and have a medial secondary vein terminating at the apex with convergent higher order laterals (Figure 5.11f). This tooth type is characteristic of the Urticales, Fagales and Betulales, which also share simple craspedodromous venation and percurrent tertiary veins. Compound teeth are particularly characteristic of the Fagales and Betulales (Hickey and Wolfe 1975). As outlined in the discussion of Morphotype 7, Morphotype 12 also has features characteristic of Nothofagus, with regularly spaced secondaries, outer secondary veins, simple craspedodromous venation, percurrent tertiaries, a toothed margin and an elliptic form (Pole 1993b,c, 1994). The tertiary venation and marginal features of this taxon are, however, clearly different to Morphotype 7, with weaker percurrent tertiary veins and different tooth architecture. The tooth architecture of Morphotype 12 is very close to living evergreen South American species such as Nothofagus nitida (illustrated in Figure 5.24c).

As discussed earlier, there have been several reports of *Nothofagus* leaves from the Late Cretaceous and Tertiary of the Antarctic Peninsula and these leaves show consistent features. Although there are similar Cretaceous forms, such as *Nothofagus cretacea* from the Santonian-Maastrichtian of King George Island (Zastawniak 1994, Dutra 1997b), these are generally too poorly preserved to allow detailed comparison. The most similar fossil is *Nothofagus oligophlebia*, described by Li (1994) from the Eocene of King George Island. It shares a similar size, form, major venation pattern and features of second and third order veins and margin with 2-4 subsidiary teeth between the major teeth, but there are differences, including the shape of the leaf apex and base. Another fossil with very similar features is *Nothofagus serrulata* from the Tertiary of Chile, with a similar form, venation pattern and marginal serrations, with two or three smaller teeth between the principal teeth, but *N. serrulata* possesses a greater number of more closely spaced secondary veins (Tanai 1986).

This morphotype includes leaves from both the Hidden Lake Formation and Santa Marta Formation. Although there is palynological support for the existence of *Nothofagus* during the Santonian-Campanian (Baldoni and Medina 1989, Baldoni 1992, Keating 1992), there have been no detailed studies of the terrestrial palynology of the earlier Coniacian-?early Santonian Hidden Lake Formation. Confirmation of botanical affinity is required, but these specimens may represent the earliest records of primitive Nothofagaceae.
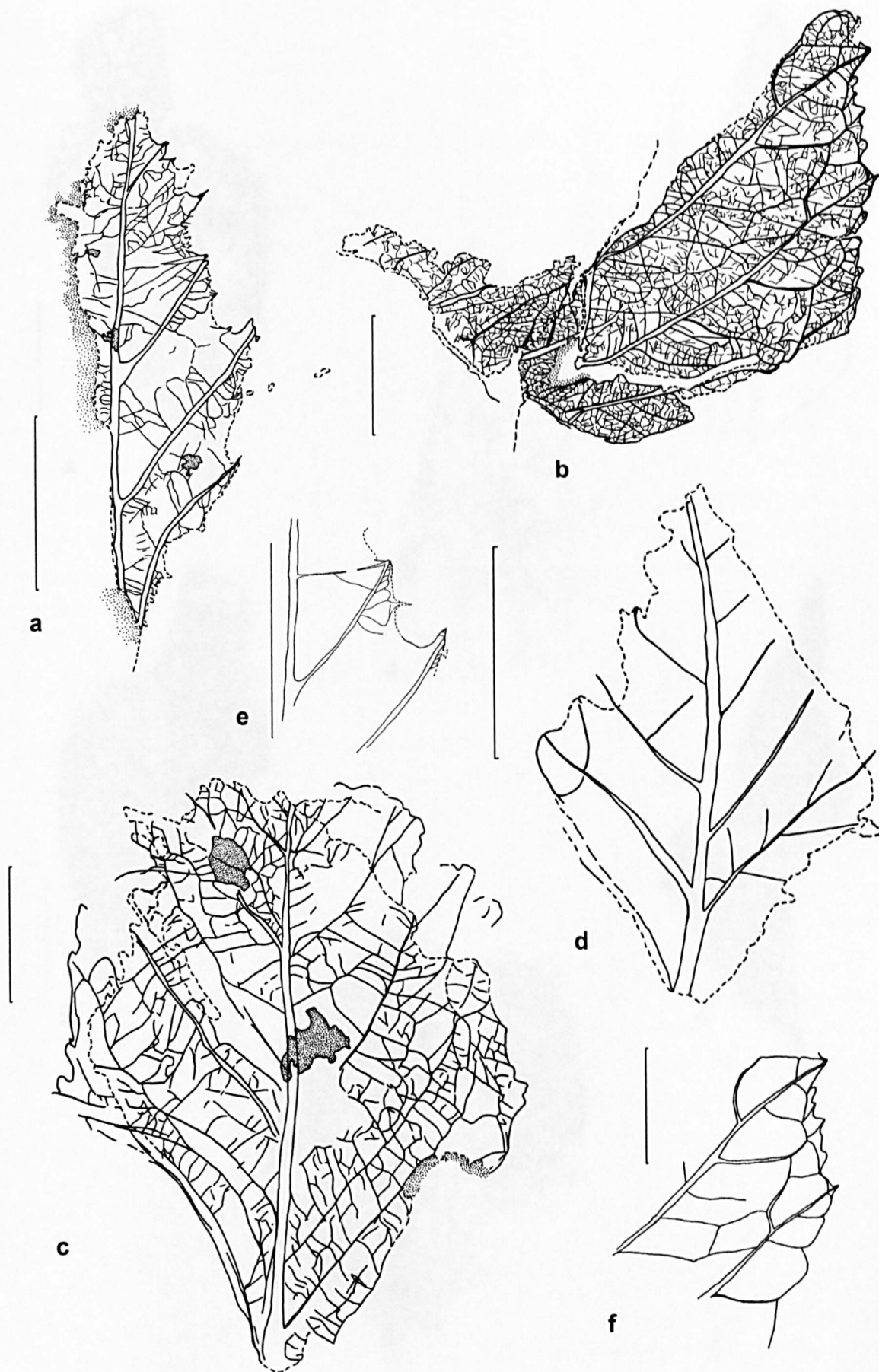
**Figure 5.11 Morphotype 12. (a) D8754.8.47a. (b) D8754.8.101a. (c) D8619.6a.
(d) D8616.74a. (e) D8754.8.47a. (f) D8754.8.101a.
Scale bar is 10mm.**
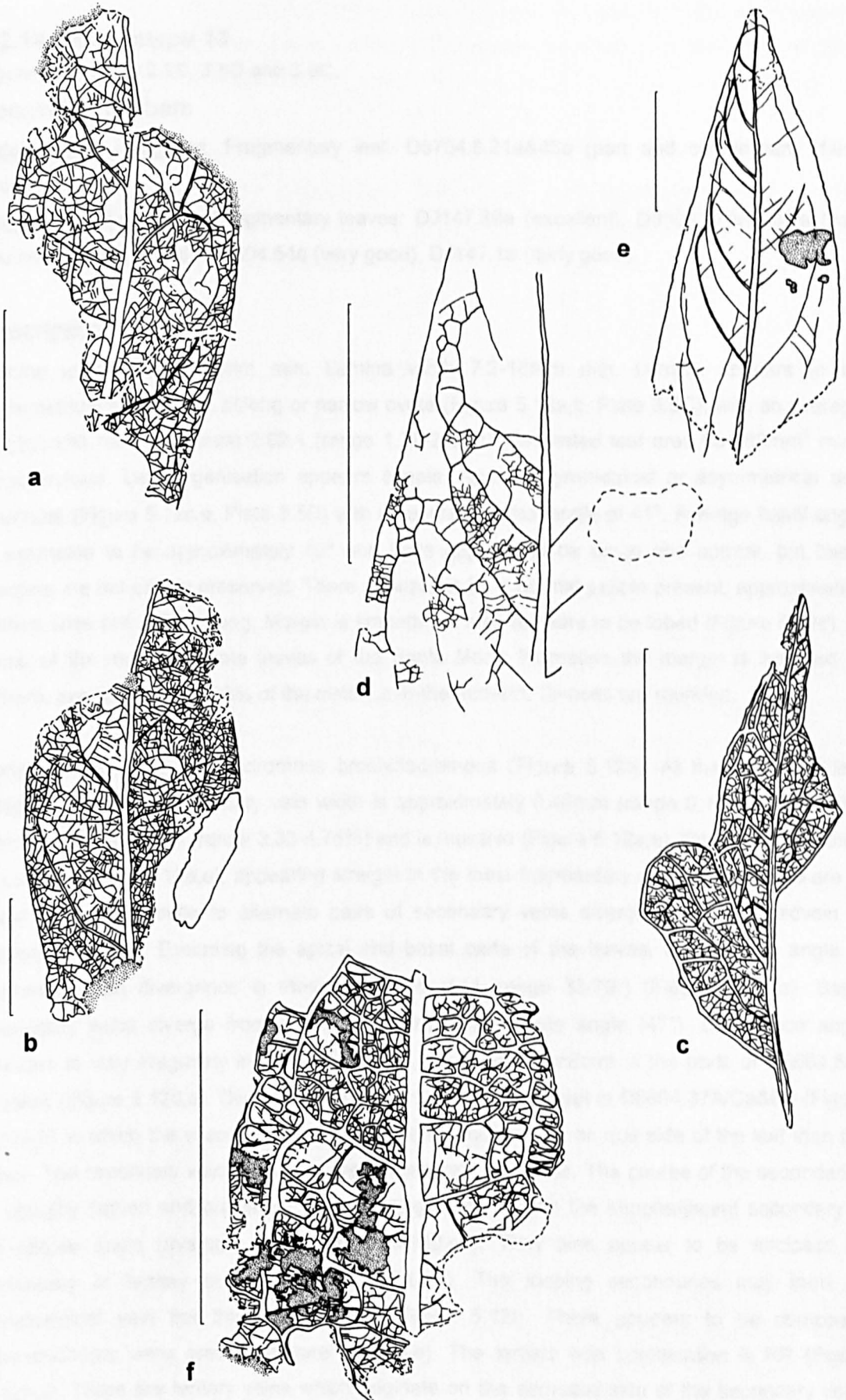
Figure 5.12 Morphotype 13. (a) D8604.37A/Ca. (b) D8604.37Ba. (c) DJ147.39a.
(d) D8604.54a. (e) D8604.54a. (f) D8754.8.21a.
Scale bar is 10mm.

5.2.14 Morphotype 13

Figure 5.12. Plate 2.2C, 3.5D and 3.9C.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.21a&46e (part and counterpart) (fairly good).

Santa Marta Formation: Fragmentary leaves: DJ147.39a (excellent), D8604.37A/Ca&Ba (part and counterpart) (good), D8604.54a (very good), DJ147.1a (fairly good).

Description

Lamina length 13.2-43.8mm min. Lamina width 7.2-18mm min. Lamina appears to be asymmetrical and form is oblong or narrow ovate (Figure 5.12a,b, Plate 3.9C), with an average length/width ratio of at least 2.02:1 (range 1.79-2.24:1). Estimated leaf area 63-482mm^2 min., microphyllous. Leaf organisation appears simple. Apex is symmetrical or asymmetrical and attenuate (Figure 5.12c,e, Plate 3.5D) with an average apical angle of 41°. Average basal angle is estimated to be approximately 80° and base appears to be acute and normal, but basal margins are not clearly preserved. There appears to be a normal petiole present, approximately 0.8mm wide and 3.8mm long. Margin is smooth but also appears to be lobed (Figure 5.12c). In some of the more complete leaves of the Santa Marta Formation the margin is indented 1-2.6mm, average 1.8mm, 33% of the distance to the midvein. Sinuses are rounded.

Venation is pinnate camptodromous brochidodromous (Figure 5.12a). At the estimated leaf midpoint, the average primary vein width is approximately 0.46mm (range 0.14-0.68mm). The average size is 4.18% (range 3.33-4.75%) and is massive (Figure 5.12a,e). Primary vein course is curved (Figure 5.12a,e), appearing straight in the most fragmentary specimens. There are at least 5-10 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 23-96°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (51°, range 33-79°) (Figure 5.12d,e). Basal secondary veins diverge from midvein at a moderate acute angle (47°). Divergence angle appears to vary irregularly in most specimens but is nearly uniform in the parts of D8604.54a present (Figure 5.12d,e). Divergence angle is symmetrical except in D8604.37A/Ca&Ba (Figure 5.12a,b) in which the secondary vein divergence is more acute on one side of the leaf than the other. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 113°) (Figure 5.12d,e,f). They also appear to be enclosed by secondary or tertiary arches (Figure 5.12a,d,e). The looping secondaries may form an intramarginal vein but this is not clear (Figure 5.12f). There appears to be composite intersecondary veins present (Figure 5.12c,d,e). The tertiary vein combination is RR (Figure 5.12a,c). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an acute angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins (Figure 5.12c). The tertiary venation pattern is random reticulate (Figure 5.12c,f). The higher order

venation is distinct (Figure 5.12d,f). The quaternary and quinternary veins are relatively randomly oriented and a fimbrial vein is present. The quaternary areoles are imperfect, random, irregular and medium-large (0.9-1.5mm).

Differential characters

This morphotype is clearly distinguished from other leaf morphotypes with pinnate camptodromous brochidodromous venation in these floras by the presence of a lobed margin, attenuate apex and massive primary vein (Figure 5.12c,e).

Discussion

A smooth lobed margin and brochidodromous venation with random reticulate tertiary veins is characteristic of the Caryophyllidae (Hickey and Wolfe 1975). However, there are no records of families from this subclass within the Antarctic Peninsula.

Cantrill and Nichols (1996) described a leaf form with brochidodromous venation and a lobed margin as *Dicotylophyllum lobatus* from the late Albian of Alexander Island. These leaves have a similar form to Morphotype 13 with very similar features of secondary and tertiary venation, including the angle of divergence of the secondaries from the midvein, the angle at which the looping secondaries join the superadjacent secondary and the tertiary venation pattern. These published leaves have a slightly different leaf apex in that the midvein does not reach the very tip of the leaf. Cantrill and Nichols (1996) referred this leaf form to the Magnoliidae or possibly the Dilleniidae.

5.2.15 Morphotype 14

Figure 5.13a,b,c,d. Plate 3.11B.

Specimen numbers

Hidden Lake Formation: Fragmentary leaves: D8754.8.67b (good), D8754.8.4c (very good), D8754.8.38a (fairly good).

Santa Marta Formation: Almost whole leaf: DJ147.53a (good).

Description

Lamina length 15.9-43.1mm min. Lamina width 12.4-34mm min. Lamina is asymmetrical and wide ovate to ovate (Figure 5.13b), with a length/width ratio of approximately 1.28-1.56:1 (average 1.42:1). Estimated leaf area 131-1094mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex appears to be asymmetrical and short acuminate (Figure 5.13a, Plate 3.11B) (apical angle approximately 59°), but the shape of the apical part of the only fossil in which the apex is preserved may have been distorted. Base appears to be obtuse and normal (Figure 5.13b,c), with an average basal angle of approximately 103°. Petiole absent or not preserved. Margin is smooth and palmately lobed (Figure 5.13b,c), indented 2.3-8.1mm, average 10.4mm, approximately 46% of distance to midvein. Sinuses are rounded.

Venation is basal, marginal perfect actinodromous (Figure 5.13a,c), with three to five primary veins diverging from the leaf base. Lateral primary veins diverge from the base at angles of 29-72° (average 44°) to the midvein and terminate in the centre of the lobes. At the estimated leaf midpoint, the average primary vein width is approximately 0.43mm (range 0.22-0.7mm). The average size is 2.2% (range 0.84-2.99%) and is stout (Figure 5.13b,c). Primary vein course is straight (Figure 5.13a). There are at least 3-4 alternate pairs of secondary veins diverging from the midvein at angles of 35-90°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (58°, range 53-63°) (Figure 5.13a). Basal secondary veins diverge from midvein at a narrow to moderate acute angle (20-47°, average 35°). The upper secondaries are more obtuse than those below. Divergence angle is more acute on one side of the leaf than the other. The secondary veins appear to be of moderate thickness. The course of the secondaries is recurved or abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an approximate right angle (average 84°). They also appear to be enclosed by secondary, tertiary, or quaternary arches (Figure 5.13a). There appears to be composite intersecondary veins present (Figure 5.13a, Appendix Volume 2 p97). The tertiary vein combination is AR (Figure 5.13a,c). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is similar to the average angle of tertiary divergence from the exmedial side of the secondary veins (Figure 5.13a). The tertiary venation pattern is random reticulate to weakly percurrent (Figure 5.13a,d). On the exmedial side of the actinodromous primaries and in the lobes, the tertiary veins form loops (Figure 5.13b,c). The course of the percurrent tertiary veins is sinuous to recurved and shows an oblique relationship to the midvein, the angle decreasing apically. Their arrangement is alternate and opposite in about equal proportions and closely spaced, with approximately 7 veins/cm. Quaternary veins appear orthogonal and marginal ultimate venation is looped (Figure 5.13a,d).

Differential characters

This morphotype is clearly distinguished from other leaves within these floras by the possession of actinodromous venation and a smooth lobed margin (Figure 5.13a,b,c, Plate 3.11B). The presence of an obtuse normal base, narrow acute divergence of the basal secondary veins, and margin characteristics differentiates it from other morphotypes with this type of venation.

Discussion

Modern leaves with entire margins and actinodromous venation occur within Dilleniidae (e.g. Santalales, Salicales) and the Cornales of the Rosidae (Hickey and Wolfe 1975). Palmately lobed leaves with actinodromous venation also occur within the Magnoliidae and leaves with similar features to Morphotype 14 occur in the Lauraceae, e.g. *Lindera triloba*, which is palmately lobed and has actinodromous venation, but differs in that the initial point of radiation of the primary veins is suprabasal.

Rees and Smellie (1989) described a trilobate leaf with an entire margin and actinodromous venation as Form F from the Cenomanian-Campanian of Williams Point, Livingston Island. The

description is very brief, but from the illustration, other similarities include the shape of the leaf base and lobes, with looping tertiaries within the lobes. However, the central lobe of Morphotype 14 appears to be wider in relation to the lateral lobes and is therefore not considered to be the same. A leaf form described by Birkenmajer & Zastawniak (1989a) as *Dicotylophyllum latitrilobatum* from the Late Cretaceous-early Tertiary of the King George Island area is the most similar to Morphotype 14. This species circumscribed *Phyllites* sp. 9 (Dusén 1908), *Sterculia* cf. *S. washburnii* (Czajkowski and Rösler 1986), *?Sterculia* (Birkenmajer and Zastawniak 1986) and an unnamed leaf form (Barton 1964) from the Late Cretaceous-Tertiary of Seymour Island and King George Island. This leaf form has perfect basal marginal actinodromous venation and a similar size, form, basal style and lobed margin. The angles of divergence of the lateral primaries and secondary veins are similar and the looping of the secondaries in the apical part of the leaf is also similar. These leaves also share the presence of intersecondary veins, random reticulate tertiaries and looping tertiaries on the exmedial side of the lateral primaries. The only difference from Morphotype 14 apparent from the illustrations is the attenuate apex and the pointed apices of the lobes. Birkenmajer and Zastawniak (1989a) suggested that the affinities of this leaf form lay with the Hamamelidae or Dilleniidae, and in particular *Cochlospermum* or *Sterculia*.

5.2.16 Morphotype 15

Figure 5.13e,f. Plate 3.7D.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.28a (good).

Description

Lamina length 34.1mm min. Lamina width 17.1mm. Lamina is slightly asymmetrical and elliptic to obovate (Figure 5.13e, Plate 3.7D), with a length/width ratio of at least 1.98:1. Estimated leaf area 387mm^2 min., microphyllous. Leaf organisation appears to be simple. Apical margin is not clearly preserved. Base appears slightly asymmetrical and acute decurrent. Petiole absent or not preserved. Margin is crenate, indented at least 1.1-1.8mm, average 1.5mm, approximately 20% of distance to midvein. Sinuses are rounded. Spacing of crenations is estimated to be 7.1-8.7mm, average 7.6mm, standard deviation 0.6mm, and spacing is described as regular.

Venation appears to be pinnate mixed craspedodromous (Figure 5.13e,f). At the estimated leaf midpoint, the primary vein width is approximately 0.4mm. The size is 3% and is stout. Primary vein course is straight. There are at least four alternate pairs of secondary veins diverging from the midvein at angles of 33-76°. Excluding the apical and basal parts of the leaf, the average angle of secondary vein divergence is 56° and the divergence angle is defined as moderate acute. Basal secondary veins diverge from midvein at a narrow acute angle (38°). The upper secondaries are more obtuse than those below and the divergence angle is more acute on one side of the leaf than the other. The secondary veins appear relatively thick, especially in the basal part of the leaf. The course of the secondaries is abruptly curved and branched. Loop-

forming branches join the superadjacent secondary at an obtuse angle (average 124°). There appears to be simple intersecondary veins present. The tertiary vein combination is AO. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. Few tertiary veins are preserved, but they appear to show a percurrent pattern. The percurrent tertiary veins are simple and sinuous and trend at an obtuse angle to the midvein. Their arrangement is opposite and they are closely spaced, with at least 4 veins/cm. Higher order venation is not clearly preserved.

Differential characters

This leaf is clearly distinguished from other leaves within these floras because it is the only specimen with pinnate mixed craspedodromous venation. It is believed that the lower two secondary veins on the left hand side of D8754.8.28a (Figure 5.13e, Plate 3.7D) terminate in the centre of crenations and that the secondaries in the apical part of the leaf form loops, as illustrated in the sketch, Figure 5.13f. However, the leaf margin and venation pattern are not clearly enough preserved for confident determination.

Discussion

Although this leaf form is clearly different from all the others within these floras, it is fragmentary which hinders comparisons with modern material. A leaf with a similar form and margin was illustrated as *Phyllites* sp. 15 from the Tertiary of Seymour Island (Dusén 1908) but there are no other fossils from the Antarctic Peninsula with similar characteristics.
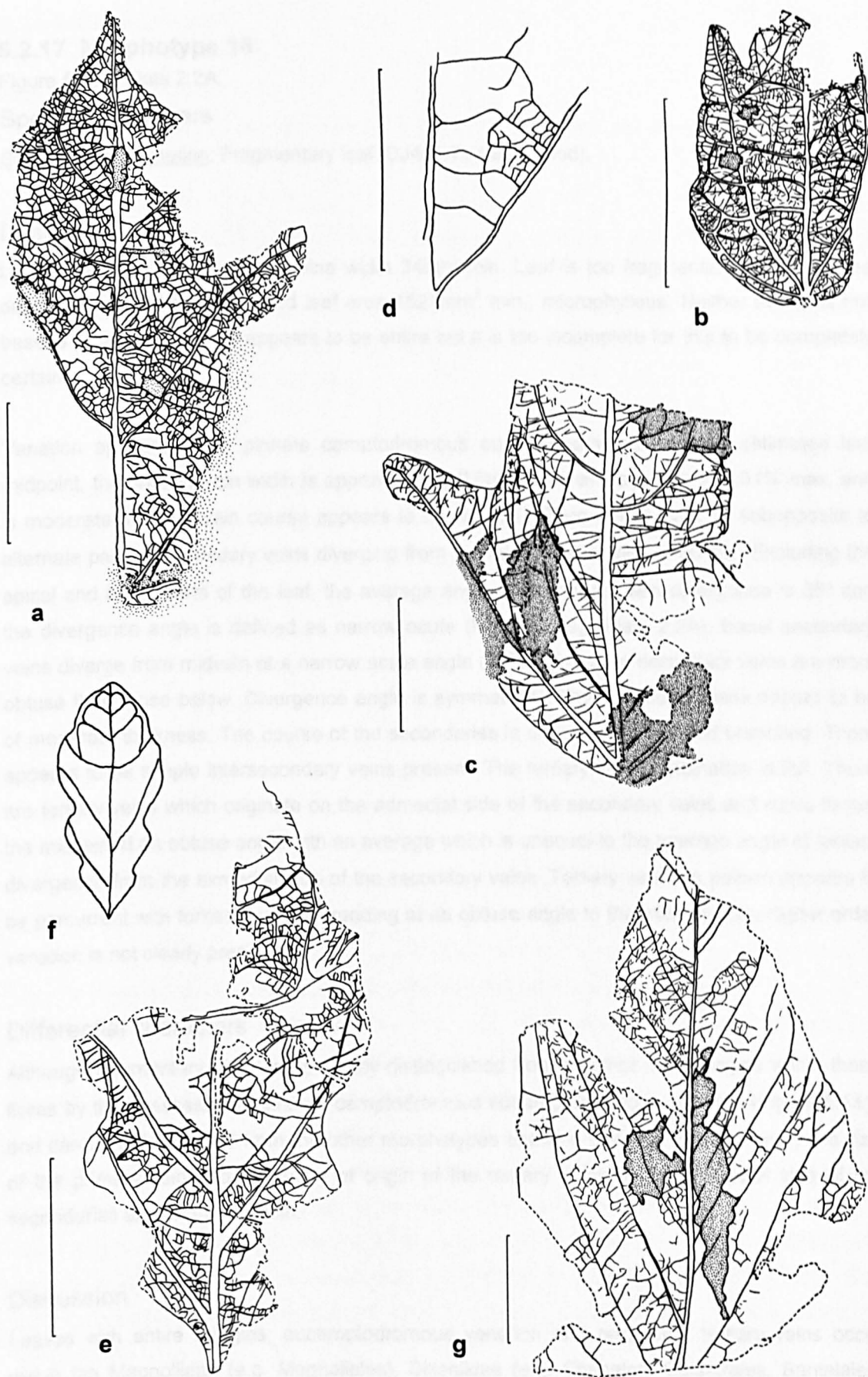
Figure 5.13 Morphotype 14. (a) D8754.8.4c. (b) D8754.8.67b. (c) DJ147.53a. (d) D8754.8.4c. Morphotype 15. (e) D8754.8.28a. (f) Interpretative diagrammatic sketch of architecture of Morphotype 15. Morphotype 16. (g) DJ451.7a. Scale bar is 10mm.

5.2.17 Morphotype 16

Figure 5.13g. Plate 2.2A.

Specimen numbers

Santa Marta Formation: Fragmentary leaf: DJ451.7a (fairly good).

Description

Lamina length 67.1mm min. Lamina width 34mm min. Leaf is too fragmentary for form to be described confidently. Estimated leaf area 1521mm^2 min., microphyllous. Neither the apex nor base is preserved. Margin appears to be entire but it is too incomplete for this to be completely certain.

Venation appears to be pinnate camptodromous eucamptodromous. At the estimated leaf midpoint, the primary vein width is approximately 0.6mm. The average size is 1.81% max. and is moderate. Primary vein course appears to be straight. There are at least 10 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 26-49°. Excluding the apical and basal parts of the leaf, the average angle of secondary vein divergence is 35° and the divergence angle is defined as narrow acute (Figure 5.13g, Plate 2.2A). Basal secondary veins diverge from midvein at a narrow acute angle (35°). The upper secondary veins are more obtuse than those below. Divergence angle is symmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is uniformly curved and branched. There appears to be simple intersecondary veins present. The tertiary vein combination is RA. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an obtuse angle with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. Tertiary venation pattern appears to be percurrent with forked tertiaries trending at an obtuse angle to the midvein. The higher order venation is not clearly preserved.

Differential characters

Although fragmentary, this leaf is clearly distinguished from all other morphotypes within these floras by the possession of pinnate camptodromous eucamptodromous venation (Figure 5.13g) and can be differentiated from the other morphotypes showing this type of venation by the size of the primary vein and the angle of origin of the tertiary veins on the admedial side of the secondaries and on the midvein.

Discussion

Leaves with entire margins, eucamptodromous venation and percurrent tertiary veins occur within the Magnoliidae (e.g. Magnoliales), Dilleniidae (e.g. Ebenales, Celastrales, Santalales) and Rosidae (Anacardiaceae) (Hickey and Wolfe 1975). Although this leaf cannot be included within any of the other morphotypes, it has not been possible to find similar forms within living or fossil leaves because of the degree of fragmentation of this Cretaceous specimen.

5.2.18 Morphotype 17

Figure 5.14a,b. Plate 3.5B.

Specimen numbers

Hidden Lake Formation: Fragmentary leaves: D8754.8.4a&5a (part and counterpart) (good).

Description

Lamina length 49.7mm min. Lamina width 26.4mm min. Lamina appears to be ovate, with a length/width ratio of about 1.9:1, but leaf is too incomplete for form to be described confidently (Figure 5.14a,b, Plate 3.5B). Estimated leaf area 799mm² min., microphyllous. Apex appears to be symmetrical and acute, with an apical angle of approximately 73°. Basal margin is not preserved. Margin appears to be entire.

Venation is described as actinodromous but these specimens are too fragmentary for venation to be clearly defined (Figure 5.14a,b). The possibility of the venation type being acrodromous or pinnate camptodromous brochidodromous cannot be eliminated. At the estimated leaf midpoint, the primary vein width is approximately 0.37mm. The size is 1.53% max. and is moderate. Primary vein course is straight. There are approximately 8 alternate pairs of secondary veins diverging from the midvein at angles of 40-67°. Excluding the apical and basal parts of the leaf, the average angle of secondary vein divergence is 58° and the divergence angle is defined as moderate acute. The basal secondary is not preserved. The upper secondaries are more acute than those below and the divergence angle is symmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 100°). There appears to be intersecondary veins present, but it is not clear whether they are simple or composite. There are three prominent enclosing, arching secondaries, segmented by other secondaries, with external looping secondaries and tertiaries. The arching secondaries are segmented by secondaries arising from the midvein and also by secondary branches diverging from the lower secondary and joining the superadjacent secondary, while the continuation of the arching secondary goes on to form another loop. The secondary arches may form an intramarginal vein. These veins roughly follow the outline of the leaf and into them the secondary and intersecondary veins merge. The tertiary vein combination is AR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an acute angle, with an average which is equal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is random reticulate to weakly percurrent. The percurrent tertiaries are simple or forked and sinuous to recurved. Their relationship to the midvein is approximately right-angled. They appear to be closely spaced, with at least 5 veins/cm. Higher order venation cannot be distinguished.

Differential characters

This fragmentary leaf is distinguished from other morphotypes within these floras by the apparent possession of actinodromous venation and differs from those with this type of venation in the acute angle of tertiary origin on the midvein and the course of the secondary veins (Figure 5.14a,b). Since the base of the leaf is incomplete and the point at which the lower branches diverge from the midvein is not preserved, the venation pattern cannot be confidently classed as actinodromous. Actinodromous venation is proposed because in the basal left hand side of D8754.8.5a (Figure 5.14b) there appears to be a vein that is thicker than the secondary veins above, radiating away from the adjacent secondary vein and the midvein. However, as stated above, the possibility that the venation pattern is acrodromous or pinnate camptodromous brochidodromous cannot be eliminated.

Discussion

The leaf is too fragmentary for comparison with modern forms because without clear preservation of the leaf base the major venation type cannot be confidently defined. However, the arching of the secondary veins is very characteristic of leaves of the Magnoiidae. There are similar living and fossil forms assigned to the Lauraceae, Monimiaceae and Annonaceae. Berry (1938) described leaves from the Tertiary of Argentina with very similar features of venation as *Anona infestans* (Annonaceae). *A. infestans* has a similar form, apex style, entire margin, tertiary venation pattern, and the secondary veins show a pattern of sweeping arches very similar to that observed in Morphotype 17. However, the fragmentary nature of Morphotype 17 prevents any further comparison.

5.2.19 Morphotype 18

Figure 5.14c. Plate 3.10B.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.26c (fair).

Santa Marta Formation: Fragmentary leaves: D8605.2a (good), DJ147.33a (fairly good), DJ147.7a (fair).

Description

Lamina length 16.1-47.4mm min. Lamina width 13.2-23.4mm min. Using measurements from best preserved specimen, D8605.2a (Figure 5.14c, Plate 3.10B), lamina appears to be oblong, with a length/width ratio of at least 2.28:1. Estimated leaf area 265-832mm^2 min., microphyllous. Leaf organisation appears simple. Apex not preserved. Leaf base is acute and cuneate and assuming base is roughly symmetrical, average basal angle is approximately 59°. Petiole absent or not preserved. Margin is entire.

Venation is pinnate camptodromous brochidodromous (Figure 5.14c, Plate 3.10B). At the estimated leaf midpoint, the average primary vein width is approximately 0.71mm (range 0.26-1.09mm). The average size is 5.56% (range 1.16-9.73%) and is massive. Primary vein course is

straight. There are at least 4 pairs of secondary veins diverging from the midvein at angles of 34-90°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (60°, range 44-78°). Basal secondary veins diverge from midvein at a narrow acute angle (34-43°, average 39°). The lowest pair of secondaries is more acute than all those above or the divergence angle is nearly uniform. Divergence angle symmetry cannot be assessed for these fragmentary specimens. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an approximate right angle (average 94°). They also appear to be enclosed by secondary and tertiary arches. The tertiary vein combination is RR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. Tertiary venation pattern is random reticulate. Higher order venation is not clearly preserved.

Differential characters

All the specimens included within this morphotype are fragmentary. These fragments cannot be included within any of the other morphotypes with pinnate camptodromous brochidodromous venation and entire margins because they possess a massive primary vein with secondary veins diverging from it at a moderate acute angle, except for the basal secondaries, which diverge at a narrow acute angle (Figure 5.14c). This combination of characters is only seen in Morphotype 3, which has pinnate camptodromous brochidodromous to eucamptodromous venation, with a different form, basal style and tertiary vein angles.

Discussion

Leaves with entire margins, pinnate camptodromous brochidodromous venation and random reticulate tertiary veins occur within the Magnoliidae (e.g. Magnoliales, Laurales, Illiciaceae), Hamamelidae (e.g. Balanopales), Caryophyllidae, and Dilleniidae (e.g. Theaceae, Thymelaeales) (Hickey and Wolfe 1975). However, the basal secondaries being more acute than all the secondary veins above is characteristic of the Laurales. Dusén (1908) illustrated a leaf with a similar shape, margin and venation pattern as *Phyllites* sp. 12 from the Tertiary of Seymour Island, but the leaf specimens of Morphotype 18 are too fragmentary for close comparison with living or fossil forms.
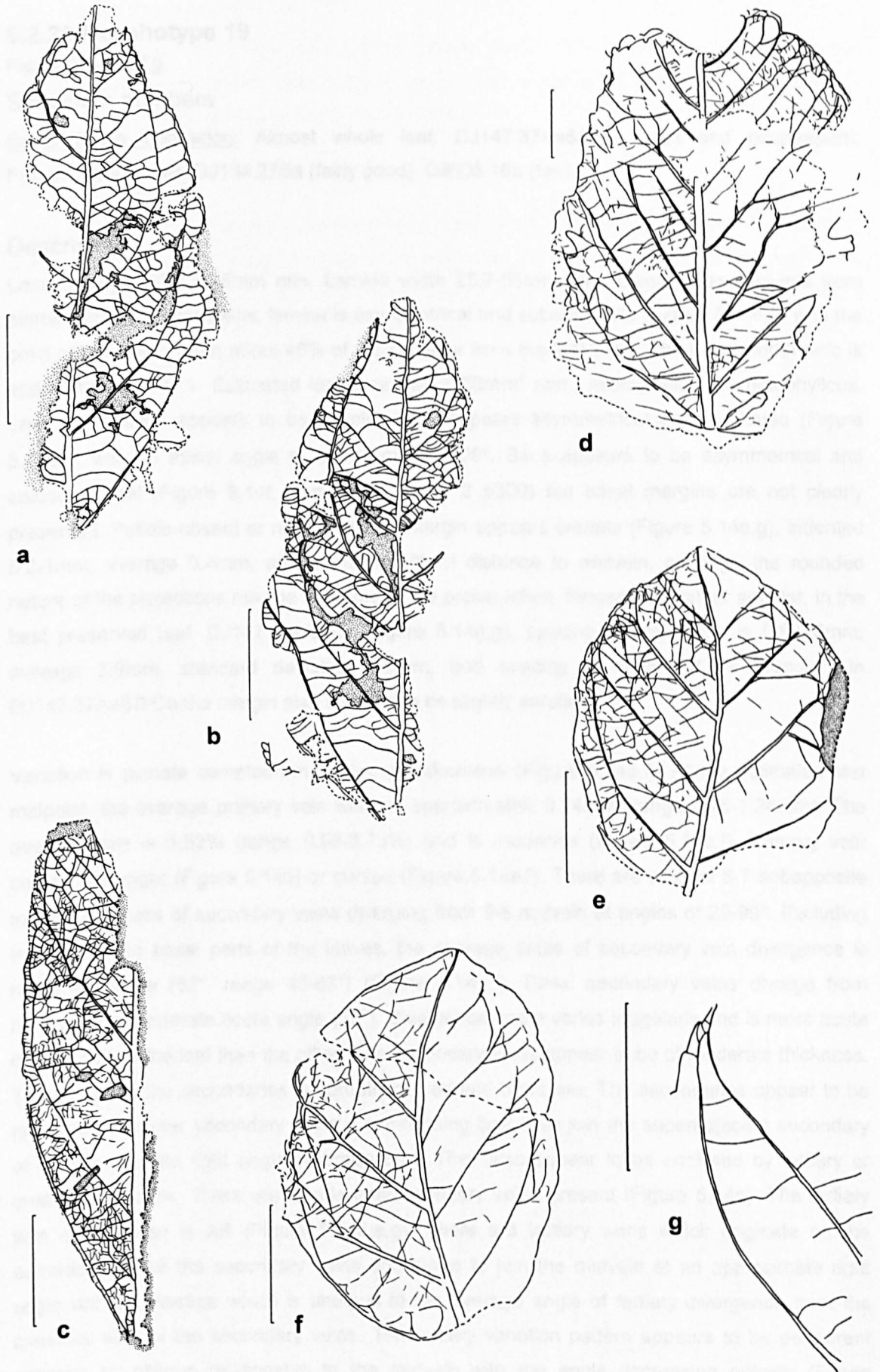
**Figure 5.14 Morphotype 17. (a) D8754.8.4a. (b) D8754.8.5a.
Morphotype 18. (c) D8605.2a.
Morphotype 19. (d) DJ134.27Ba. (e) DJ147.37Aa.
(f) DJ147.37B/Ca. (g) DJ147.37Aa. Scale bar is 10mm.**

5.2.20 Morphotype 19

Figure 5.14d,e,f,g.

Specimen numbers

Santa Marta Formation: Almost whole leaf: DJ147.37Aa&B/Ca (part and counterpart). Fragmentary leaves: DJ134.27Ba (fairly good), D8605.16a (fair).

Description

Lamina length 33.2-65.5mm min. Lamina width 25.7-55mm min. Using measurements from almost complete specimens, lamina is asymmetrical and suborbiculate (Figure 5.14e,f), with the point of maximum width about 46% of the distance from the leaf base. The length/width ratio is approximately 1.37:1. Estimated leaf area 569-2763mm^2 min., microphyllous to notophyllous. Leaf organisation appears to be simple. Apex appears asymmetrical and is obtuse (Figure 5.14e,f), with an apical angle of approximately 109°. Base appears to be asymmetrical and obtuse normal (Figure 5.14f, Appendix Volume 2 p300) but basal margins are not clearly preserved. Petiole absent or not preserved. Margin appears crenate (Figure 5.14e,g), indented 0.2-1mm, average 0.4mm, approximately 4% of distance to midvein, although the rounded nature of the projections may be a feature of the preservation. Sinuses are rather angular. In the best preserved leaf, DJ147.37A/B&C (Figure 5.14e,g), spacing of crenations is 0.9-6.8mm, average 2.9mm, standard deviation 1.9mm, and spacing is described as irregular. In DJ147.37Aa&B/Ca the margin also appears to be slightly enrolled.

Venation is pinnate camptodromous brochidodromous (Figure 5.14e,f). At the estimated leaf midpoint, the average primary vein width is approximately 0.74mm (range 0.45-1.24mm). The average size is 1.82% (range 0.98-2.73%) and is moderate (Figure 5.14e,f). Primary vein course is straight (Figure 5.14d) or curved (Figure 5.14e,f). There are at least 6-7 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 29-99°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (52°, range 45-63°) (Figure 5.14e,f). Basal secondary veins diverge from midvein at a moderate acute angle (46°). Divergence angle varies irregularly and is more acute on one side of the leaf than the other. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and branched. The secondaries appear to be provided with outer secondary veins. Loop-forming branches join the superadjacent secondary at an approximate right angle (average 80°). They also appear to be enclosed by tertiary or quaternary arches. There are simple intersecondary veins present (Figure 5.14e). The tertiary vein combination is AR (Figure 5.14d,e,g). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern appears to be percurrent showing an oblique relationship to the midvein with the angle decreasing apically (Figure 5.14d,g). The higher order venation is not clearly preserved. The crenations appear to be served by deflected tertiary veins following a central course (Figure 5.14g).

Differential characters

This morphotype is clearly distinguished from other leaf morphotypes with pinnate camptodromous brochidodromous venation within these floras by the presence of a non-entire margin, obtuse apex and elliptic form (Figure 5.14e,g).

Discussion

There are leaves with pinnate camptodromous brochidodromous venation, percurrent tertiaries and non-entire margins within the Magnoliidae (e.g. Monimiaceae, Trimeniaceae, Illiciales), the Rosidae (e.g. Burseraceae) and the Dilleniidae (Hickey and Wolfe 1975). The Dilleniidae includes leaves with brochidodromous secondary venation, weakly percurrent tertiaries and in some groups the toothed leaf margins become enrolled during ontogeny (e.g. Theaceae, Caryocaraceae, some Ericales). The leaves of Morphotype 19 may be considered similar to those of this group in that they possess brochidodromous venation and percurrent tertiary veins, but in addition, the non-entire leaf margin in D8754.8.37Aa&B/Ca (Figure 5.14e,f) appears slightly enrolled. The style of preservation, however, means that this is not a confident determination.

Dusén (1908) illustrated similar leaves from the Tertiary of Seymour Island as *Phyllites* sp. 2. These leaves appear to share a crenate margin, brochidodromous venation and a similar angle of secondary vein divergence, but the Seymour Island specimens possess insufficient detail for any further comparison.

5.2.21 Morphotype 20
Figure 5.15. Plates 2.1B, 3.3C and 3.9B.
Specimen numbers

Hidden Lake Formation: Fragmentary leaves: D8754.8.30a (good), D8754.8.31a (fairly good).
Santa Marta Formation: Fragmentary leaf: DJ147.55Aa&Ba (part and counterpart) (good).

Description

Lamina length 20.5-39.5mm min. Lamina width 16.8-21.3mm min. Lamina appears to be slightly asymmetrical and oblong (Figure 5.15e, Plate 3.9B) to elliptic (Figure 5.15d, Plate 3.3C) but the specimens are too fragmentary for form to be confidently described. Estimated leaf area 230-561mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex is acute (Figure 5.15a), with an apical angle of approximately 77°. Base appears to be obtuse (basal angle approximately 150°), possibly cordate (Figure 5.15d), but basal margins are incomplete so this is not completely clear. Margin is crenate (Figure 5.15f,g), indented 0.1-1.1mm, average 0.4mm, approximately 7% of distance to midvein. Sinuses appear quite angular in the Hidden Lake Formation leaves (Figure 5.15f,g) but are rounded in the Santa Marta Formation specimens (Figure 5.15a). Crenation spacing is 0.7-10.6mm, average 3.8mm. For each leaf, standard deviation of spacing measurements is 0.4-2.5mm and spacing is described as irregular.

Venation is pinnate semicraspedodromous (Figure 5.15a,b,e,h). At the estimated leaf midpoint, the average primary vein width is approximately 0.5mm (range 0.43-0.56mm). The average size is 2.76% (range 2.42-3.14%) and is stout (Figure 5.15d). Primary vein course is straight or curved. There are at least 4-8 opposite or alternate pairs of secondary veins diverging from the midvein at angles of 48-135°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is wide acute (72°, range 68-76°) (Figure 5.15a,b,d). Basal secondary veins are too poorly preserved for their divergence angle to be measured. Divergence angle varies irregularly and is more acute on one side of the leaf than the other. The secondary veins appear relatively fine to moderate. The course of the secondaries is abruptly curved and branched. The secondary veins appear to be provided with outer secondaries. Loop-forming branches join the superadjacent secondary at an acute angle (average 68°) (Figure 5.15a,b,e). There appears to be simple intersecondary veins present (Figure 5.15d). The tertiary vein combination is AR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is similar to the average angle of tertiary divergence from the exmedial side of the secondary veins. Tertiary venation pattern appears to be random reticulate to weakly percurrent but is not clearly preserved (Figure 5.15a,b,c). The higher order venation cannot be distinguished. The apical parts of the crenations contain darker material, which may point to the presence of glands (Figure 5.15e). The principal vein of each crenation is a secondary vein showing a central and direct course. The accessory veins are looped (Figure 5.15f,g).

Differential characters

This morphotype is distinguished from most other leaf morphotypes within these floras by the possession of pinnate semicraspedodromous venation (Figure 5.15a,b,e,h) and a crenate margin (Figure 5.15f,g). It differs from Morphotype 4, which also shows this type of venation, by the wide acute angle of divergence of the secondaries from the midvein and the presence of outer secondary veins.

Discussion

Leaves with semicraspedodromous venation and a non-entire margin occur within the Magnoliidae (Chloranthaceae), the Hamamelidae (Myricales) and many orders of the Rosidae, however the leaves of Morphotype 20 possess characteristics of the Dilleniidae (Hickey and Wolfe 1975). The crenations in Morphotype 20 are most similar to the tooth forms observed in the Dilleniidae, such as the violoid, salicoid or malvoid tooth types. These similarities include the central course of the principal vein, the looping accessory veins and the possible presence of glands in the tooth apices (Figure 5.15e,f,g). Similar groups within the Dilleniidae with pinnate semicraspedodromous venation, random reticulate to weakly percurrent tertiaries and similar marginal characteristics include the Violales, Passiflorales, Salicales, and Malvales.

Rees and Smellie (1989) described leaves with semicraspedodromous venation and a serrate margin (Form E) from the Cenomanian-Campanian of Williams Point, Livingston Island. These are not well preserved but from the illustration, the secondaries are more regularly spaced and

form more regular loops closer to the margin than Morphotype 20. Dusén (1908) illustrated several leaves with similar features to these James Ross Island specimens from the Tertiary of Seymour Island, referring leaves with a similar form and venation pattern to the Proteaceae, but these Tertiary leaves are too poorly preserved for detailed comparison. The leaves described as *Monimiophyllum antarcticum* from the Tertiary of King George Island (Birkenmajer and Zastawniak 1989a) are similar to Morphotype 20 in that they possess an oblong form, semicraspedodromous venation, a stout midvein, irregularly spaced secondary veins diverging from the midvein at a wide acute angle and random reticulate tertiary venation. However, the marginal teeth show different characteristics and are considered monimioid in *M. antarcticum*.

Pole (1993d) described leaves from the Miocene of New Zealand with suggested affinities to the Elaeocarpaceae. These leaves have a similar form to Morphotype 20 and variable venation patterns, appearing semicraspedodromous in some of the illustrated material. This leaf form is similar to Morphotype 20 in that it possesses irregularly spaced subopposite to alternate pairs of secondary veins, with glandular teeth fed by secondary veins and outer secondary veins. However, the Miocene leaves differ from Morphotype 20 in the possession of a cuneate base and spines in the tooth apices. Zastawniak (1994) described a fragmentary leaf from the Santonian-Maastrichtian of King George Island as *Dicotylophyllum* sp. 10 and suggested that it showed similarities to the Elaeocarpaceae. The similarities with Morphotype 20 described for *Dicotylophyllum* sp. 10 include a probable toothed margin, stout primary vein, and irregularly spaced, curved secondary veins with simple intersecondary veins and at least two secondary vein branches on the exmedial side of the secondary veins. The angle of divergence differs in that it is described as moderate acute in *Dicotylophyllum* sp. 10, but the King George Island material is too poorly preserved for further comparison. There are palynological records of the Elaeocarpaceae on the Antarctic Peninsula, but only from the Eocene of Seymour Island (Askin 1997).

Modern leaves of the Elaeocarpaceae also show similarities to Morphotype 20. For example, *Elaeocarpus arnhemicus* has an oblong to elliptic form with semicraspedodromous venation and rather rounded glandular teeth fed by secondary vein branches. The secondary veins diverge from the midvein at a moderate to wide acute angle and the loop-forming branches join the superadjacent secondary at an acute angle. The tertiaries also appear to show a similar pattern to Morphotype 20, arising from the secondary veins and joining the midvein at similar angles. However, the high magnification photographs of *Elaeocarpus* illustrated by Pole (1993d) show that extant species also possess spines in the tooth apices. It is possible that the teeth of Morphotype 20 originally possessed spines that were not preserved. The acute cuneate base observed in *E. arnhemicus* does not rule out affinity with the Elaeocarpaceae, since basal style is very variable within the Elaeocarpaceae and even within *Elaeocarpus*. *Elaeocarpus culminicola*, for example, compares well with Morphotype 20 in the features outlined above, and also possesses a rounded obtuse base. The teeth of *Elaeocarpus grahamii* also appear irregularly compound as in Morphotype 20. Possible affinities with the Elaeocarpaceae are therefore suggested for Morphotype 20.
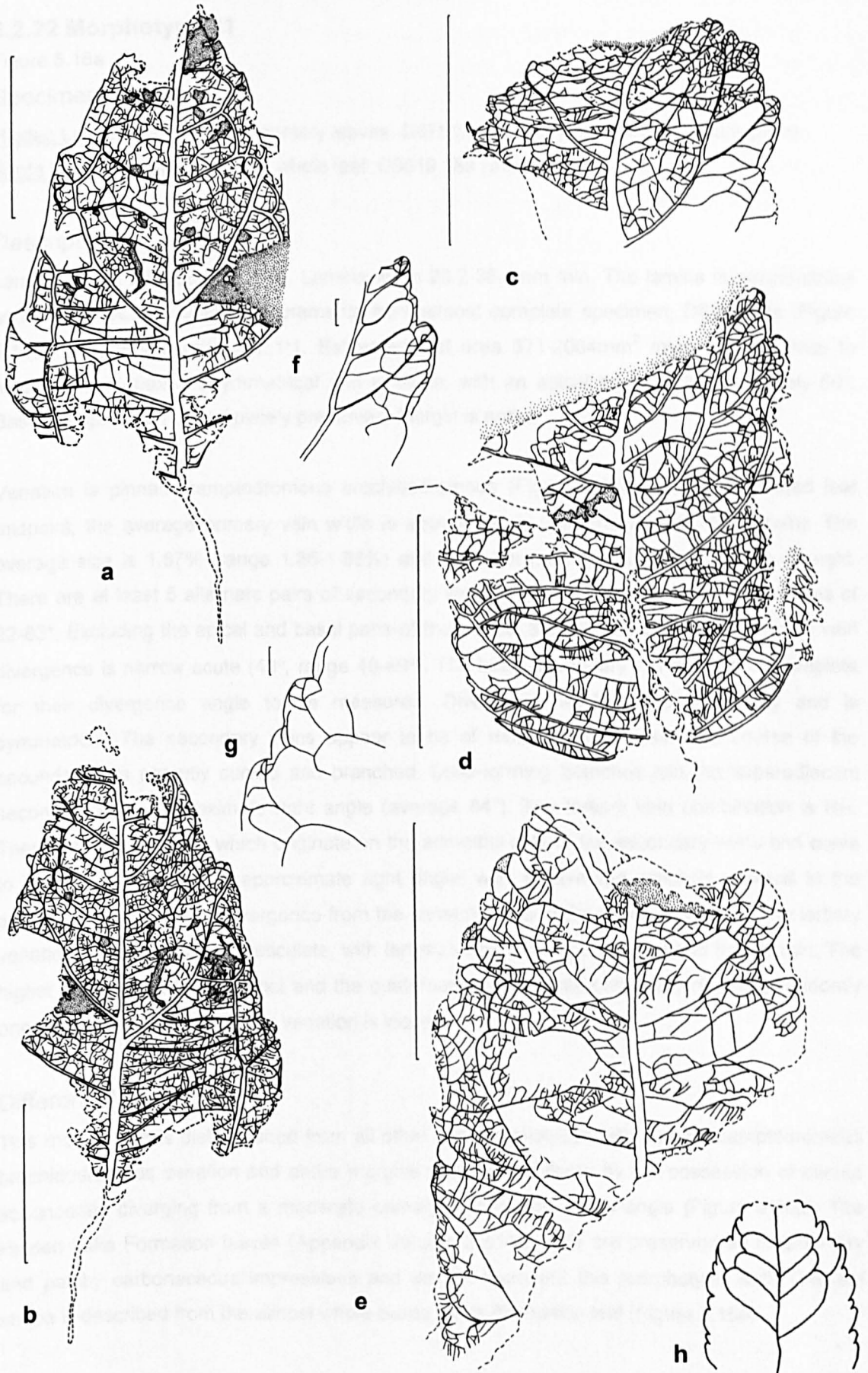
Figure 5.15 Morphotype 20. (a) DJ147.55Aa. (b) DJ147.55Ba. (c) D8754.8.30a.
(d) D8754.8.30a. (e) D8754.8.31a. (f) D8754.8.30a. (g) D8754.8.31a.
(h) Interpretative diagrammatic sketch of the venation pattern in D8754.8.31a.
Scale bar is 10mm in (a),(b),(c),(d) and (e). Scale bar is 1mm in (f) and (g).

5.2.22 Morphotype 21

Figure 5.16a.

Specimen numbers

<u>Hidden Lake Formation</u>: Fragmentary leaves: D8754.8.98b (fair), D8754.8.47b (fairly poor).
<u>Santa Marta Formation</u>: Almost whole leaf: D8619.18a (excellent).

Description

Lamina length 20.5-69.8mm min. Lamina width 20.2-38.4mm min. The lamina is asymmetrical and narrow ovate. Using measurements from almost complete specimen, D8619.18a (Figure 5.16a), length/width ratio is 2.1:1. Estimated leaf area 571-2064mm^2 min., microphyllous to notophyllous. Apex is asymmetrical and is acute, with an apical angle of approximately 56°. Basal margins are not completely preserved. Margin is entire.

Venation is pinnate camptodromous brochidodromous (Figure 5.16a). At the estimated leaf midpoint, the average primary vein width is approximately 0.58mm (range 0.48-0.7mm). The average size is 1.87% (range 1.86-1.88%) and is moderate. Primary vein course is straight. There are at least 5 alternate pairs of secondary veins diverging from the midvein at angles of 22-83°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is narrow acute (43°, range 40-49°). The basal secondary veins are too incomplete for their divergence angle to be measured. Divergence angle varies irregularly and is symmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an approximate right angle (average 84°). The tertiary vein combination is RR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is random reticulate, with tertiary veins forming loops close to the margin. The higher order venation is distinct and the quaternaries and quinternaries are relatively randomly oriented. The marginal ultimate venation is looped.

Differential characters

This morphotype is distinguished from all other leaf morphotypes with pinnate camptodromous brochidodromous venation and entire margins within these floras by the possession of curved secondaries diverging from a moderate primary at a narrow acute angle (Figure 5.16a). The Hidden Lake Formation leaves (Appendix Volume 2 p112, 146) are preserved as fragmentary and patchy carbonaceous impressions and do not represent this morphotype well. The leaf shape is described from the almost whole Santa Marta Formation leaf (Figure 5.16a).

Discussion

Leaves with entire margins, pinnate camptodromous brochidodromous venation and random reticulate tertiary veins occur within the Magnoliidae (e.g. Magnoliales, Laurales, Illiciaceae),

Hamamelidae (e.g. Balanopales), Caryophyllidae, and Dilleniidae (e.g. Theaceae, Thymelaeales) (Hickey and Wolfe 1975). Dusén (1908) illustrated leaves with entire margins, brochidodromous venation and similar secondary vein divergence angles from the Tertiary of Seymour Island as *Leguminosites*, with possible affinities to the Fabaceae. These leaves are, however, too poorly preserved for detailed comparison with the James Ross Island specimens. Zastawniak (1994) also noted that the application of the name *Leguminosites* was misleading because there are many leaves of similar shape and venation to those of the Fabaceae.

5.2.23 Morphotype 22

Figure 5.16b.

Specimen numbers

<u>Santa Marta Formation</u>: Fragmentary leaf: D8605.30a (good).

Description

Lamina length 64.9mm min. Lamina width 28.6mm. The lamina is asymmetrical and appears to be narrow ovate with a length/width ratio of at least 2.27:1, but the leaf is incomplete. Estimated leaf area 1237mm^2 min., microphyllous. Apex appears roughly symmetrical and acute, with an apical angle of approximately 54°. Base is not preserved. Margin is entire (Figure 5.16b).

Venation is pinnate camptodromous brochidodromous (Figure 5.16b). At the estimated leaf midpoint, the primary vein width is approximately 0.76mm. The size is 2.81% and is stout. Primary vein course appears to be straight. There are at least 17 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 39-90°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (53°). The basal secondary veins are not preserved. Divergence angle varies irregularly and is symmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and unbranched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 129°). There is a clear intramarginal vein present. The tertiary vein combination appears to be RR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an obtuse angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation may be weakly percurrent but is not clearly preserved. The higher order venation cannot be distinguished, except for the marginal ultimate venation, which is looped.

Differential characters

This leaf is different from all the other morphotypes because it is the only one with regularly spaced secondary veins and a clear intramarginal vein (Figure 5.16b). It can also be distinguished from all other leaves with pinnate camptodromous brochidodromous venation by the obtuse angle of origin of tertiary veins on the midvein.

Discussion

Entire margined leaves with brochidodromous venation and intramarginal veins are characteristic of leaves of the Dilleniidae, including the Primulales and Myrtales. The Myrtales are usually considered to be within the Rosid subclass but were included within the Dilleniidae based on leaf architectural features by Hickey and Wolfe (1975). The presence of an intramarginal vein is considered especially characteristic of the Myrtaceae. The shape and venation in Morphotype 22 is very similar to genera of modern Myrtaceae, such as *Metrosideros*. For example, *Metrosideros robusta* (Figure 5.24d) shows similarities to Morphotype 22 including an acute apex, entire margin and brochidodromous venation with a clear intramarginal vein. Numerous subopposite to alternate pairs of secondary veins diverge from the straight midvein at a moderate acute angle. It is also possible that the tertiary venation pattern observed in *M. robusta* is similar to that in the Cretaceous fossil, but the tertiary veins are not well defined in Morphotype 22.

Zastawniak (1994) described leaves of *Myrciophyllum santacruzensis* assigned to the Myrtaceae from the Santonian-Maastrichtian of King George Island. These fragmentary specimens are similar to Morphotype 22 in the possession of brochidodromous venation with a distinct intramarginal vein and numerous closely spaced secondary veins diverging from the midvein at a moderate to wide acute angle. *M. santacruzensis* is lorate, with a length/width ratio of at least 6:1, but since Morphotype 22 is only a fragment from the apical part of a leaf it is possible that the original leaf showed a much greater length/width ratio. Morphotype 22 may therefore be similar to *M. santacruzensis* but is too fragmentary for confident determination. There is support for the presence of Myrtaceae within the Santa Marta Formation from palynological samples studied by Baldoni (1992).

5.2.24 Morphotype 23

Figure 5.16c,d.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.49b (fair).

Santa Marta Formation: Almost whole leaf: D8625.119a (good). Fragmentary leaf: DJ134.11a (fairly poor).

Description

Lamina length 18.2-58.6mm min. Lamina width 14.8-46.4mm min. Lamina appears to be asymmetrical and wide ovate (Figure 5.16c), with a length/width ratio of at least 1.26:1. Estimated leaf area 184-1379mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex is not preserved. Base appears to be asymmetrical and obtuse normal (Figure 5.16d), with an average basal angle of approximately 93°. Petiole absent or not preserved. Margin is toothed, indented 0.2-2.1mm, average 1.3mm, approximately 8% of distance to midvein. Teeth are described as simple, although it appears that they may be compound with two size classes of teeth in the Hidden Lake Formation specimen, D8754.8.49b (Figure 5.16d). Teeth are serrate

and average apical angle is obtuse (87-146°, average 121°). Dominant serration type is straight on basal side and straight on apical side. Sinuses appear quite rounded. The margin is best preserved in D8754.8.49b and in this specimen tooth spacing is 0.9-8.6mm, average 3.4mm, standard deviation 2.4mm, and spacing is described as irregular.

Venation appears to be pinnate simple craspedodromous (Figure 5.16c). At the estimated leaf midpoint, the average primary vein width is approximately 0.42mm wide (range 0.26-0.65mm). The size is approximately 1.5% and is moderate (Figure 5.16c). The primary vein size in D8754.8.49a (Figure 5.16d) appears to be weak but this leaf is too poorly preserved for accurate measurement. The primary vein course appears to be straight and unbranched. There are at least 2 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 32-58°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (46°, range 41-50°) (Figure 5.16c). Basal secondary veins diverge from midvein at a moderate acute angle (56-58°, average 57°). The upper secondaries appear to be more acute than those below but these specimens are too fragmentary for the variation in divergence angle along the length of the lamina to be described confidently. Divergence angle is more acute on one side of the leaf than the other. The secondary veins appear to be of moderate thickness. The course of the secondaries is straight to uniformly curved and unbranched. The tertiary vein combination is AR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an obtuse angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is percurrent and these tertiary veins are simple and straight to sinuous (Figure 5.16c). They show an oblique relationship to the midvein and they appear distantly spaced with 2-3 veins/cm. Higher order venation cannot be distinguished.

Differential characters

This morphotype is distinguished from other leaf morphotypes within these floras by the presence of pinnate simple craspedodromous venation (Figure 5.16c,d). The possession of simple teeth, along with a moderate primary vein and different tertiary vein angles of origin differentiate the fragmentary specimens of Morphotype 23 from other morphotypes within the floras with simple craspedodromous venation.

Discussion

Leaves with a similar simple craspedodromous venation pattern, toothed margins and percurrent tertiary veins occur within the Hamamelidae (e.g. Ulmaceae, Fagales, Betulales), Dilleniidae (e.g. Dilleniaceae, Actinidiaceae, Saurauiaceae, Aquifoliaceae) and the Rosidae (e.g. Davidsoniaceae, Brunelliaceae, Oleales) (Hickey and Wolfe 1975). The leaves of Morphotype 23 are too poorly preserved for determination of tooth type, which would have aided in assessing possible affinities to extant taxa. However, the lack of evidence for glands or spines in the tooth apices may indicate that this morphotype is most similar to the Hamamelid groups.

Cretaceous leaves with pinnate simple craspedodromous venation have been included under the Protophyll morphotype (Crabtree 1987, Zastawniak 1994), but Morphotype 23 does conform to the criteria outlined for the recognition of *Nothofagus*. These criteria are the possession of regularly spaced secondary veins, outer secondary veins, simple craspedodromous venation, percurrent tertiary veins, a toothed margin and an ovate form, along with an association with *Nothofagus* pollen (Pole 1993b,c, 1994, Scriven *et al.* 1995). Fossil leaf forms from the Antarctic Peninsula (and Chile) that are very similar to Morphotype 23 have been described as *Nothofagus subferruginea*, which is considered most similar to extant deciduous *Nothofagus alessandri* from South America (Tanai 1986). Similarities between the two leaf forms include the ovate form, asymmetrical, obtuse base, outer secondary veins, percurrent tertiary veins and margin with simple serrations. *N. subferruginea* has been recorded from the Campanian-Miocene of King George Island (Birkenmajer and Zastawniak 1989a, Li 1994) and the illustration of the Cretaceous material provided by Birkenmajer and Zastawniak (1989a) shows a similar leaf margin and secondary vein divergence to Morphotype 23. Leaves that have also been compared to *N. subferruginea* include *Fagus obscura* from the Tertiary of Seymour Island (Dusén 1908) and leaves such as *Nothofagus ulmifolia* and *N.* aff. *alessandri* from the Tertiary of King George Island (Barton 1964, Zastawniak 1981, Zastawniak *et al.* 1985, Czajkowski and Rösler 1986). However, despite the apparent similarity between the Late Cretaceous leaves illustrated by Birkenmajer and Zastawniak (1989a) and Morphotype 23, Tanai (1986) states that leaves of this species possess nearly straight secondary veins which abruptly arise up along the basal side of the tooth to end in the tooth apex. The secondary veins do not appear to end in the tooth apices in Morphotype 23.

As stated previously, there have been numerous reports of leaves similar to those of *Nothofagus* on the Cretaceous-Tertiary Antarctic Peninsula. Dutra *et al.* (1998) reported a flora of possible Campanian age from Nelson Island, dominated by *Nothofagus* leaves. These leaves appear very similar to those of Morphotype 23, but the preservation of the Nelson Island material combined with the fragmentation of these James Ross Island leaves does not allow detailed comparison. Morphotype 23 also appears very similar to leaves assigned to *Nothofagus cretacea* and *Nothofagus* sp. by Zastawniak (1994) and Dutra (1997b) from the Santonian-Maastrichtian of King George Island. Similarities include the ovate form, angle of divergence of the secondary veins and character of the percurrent tertiaries, but the marginal details of *N. cretacea* are insufficiently preserved for close comparison. Other leaf forms assigned to *Nothofagus* from the Cretaceous-Tertiary of the Antarctic Peninsula too poorly preserved for comparison with the James Ross Island material have already been noted in the discussion of Morphotype 7.
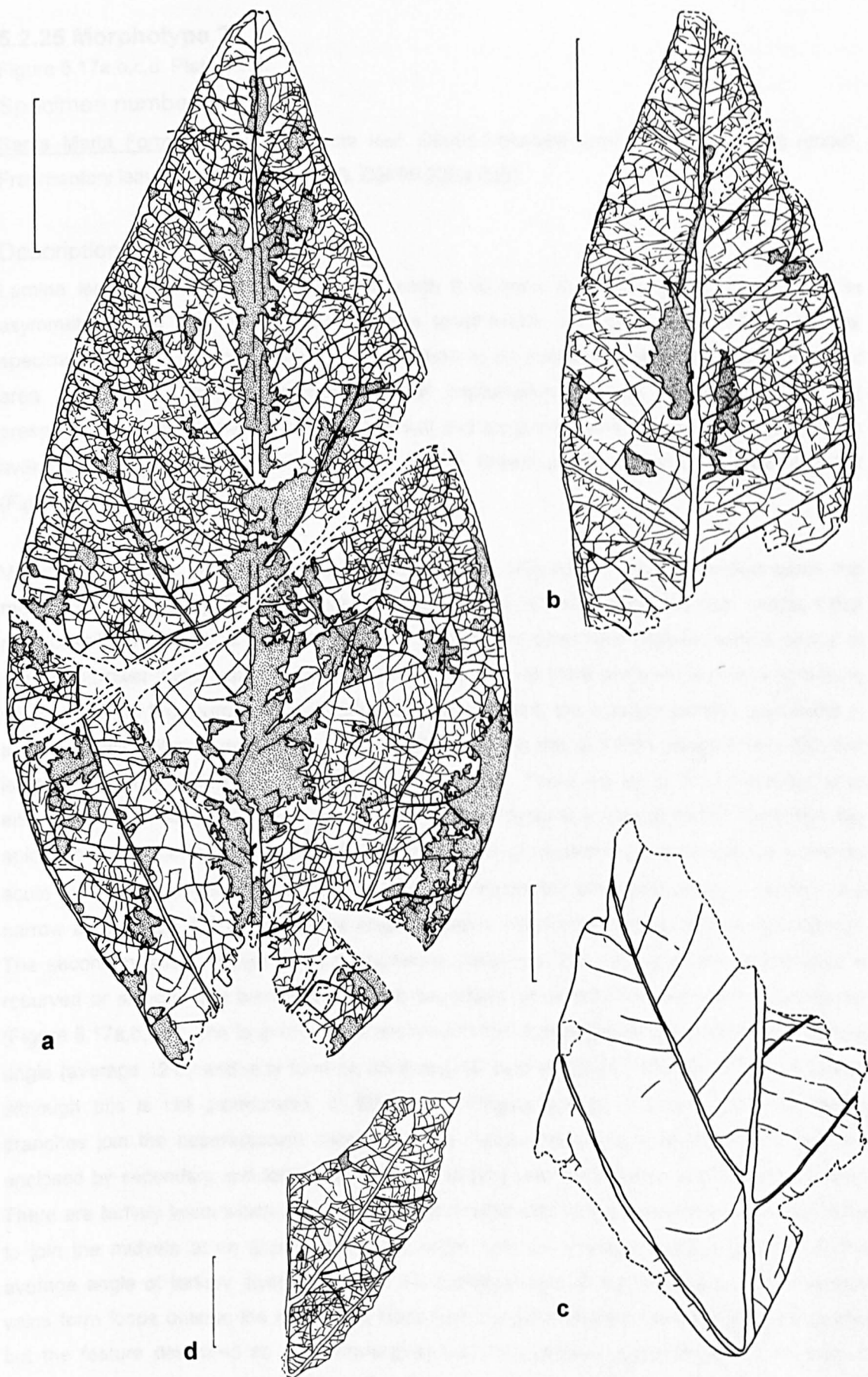
Figure 5.16 Morphotype 21. (a) D8619.18a. Morphotype 22. (b) D8605.30a.
Morphotype 23. (c) D8625.119a. (d) D8754.8.49b.
Scale bar is 10mm.

5.2.25 Morphotype 24

Figure 5.17a,b,c,d. Plate 3.7C.

Specimen numbers

Santa Marta Formation: Almost whole leaf: D8605.21Aa&Ba (part and counterpart) (good). Fragmentary leaves: D8604.39a (good), D8605.22Ba (fair).

Description

Lamina length 6.3-51.2mm min. Lamina width 6-33.4mm min. The lamina appears to be asymmetrical and obovate, with an average length/width ratio of at least 1.04:1, but the specimens are too incomplete for the lamina form to be confidently described. Estimated leaf area 25-1139mm^2 min., microphyllous. Leaf organisation appears simple. Apex is not preserved. Base is symmetrical or asymmetrical and acute decurrent (Figure 5.17a,b,c) with an average basal angle of approximately 62°. Petiole absent or not preserved. Margin is entire (Figure 5.17a,b).

Venation is pinnate camptodromous brochidodromous (Figure 5.17b,c,d). Included within this morphotype is a leaf (D8604.39a, Figure 5.17a, Plate 3.7C) with rather unusual venation that may possibly represent a separate taxon. There is one prominent midvein with a series of slightly narrower veins branching dichotomously from it and there are several orders of looping veins nearer to the margin. At the estimated leaf midpoint, the average primary vein width is approximately 0.59mm (range 0.15-1.02mm). The average size is 3.08% (range 2.05-4.3%) and is stout (Figure 5.17a). Primary vein course is straight. There are up to 5-12 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 18-68°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is narrow acute (33°, range 26-39°) (Figure 5.17b,c,d). Basal secondary veins diverge from midvein at a narrow acute angle (30°). Divergence angle is nearly uniform to irregular and is symmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is recurved or sinuous and branched, with the secondary veins provided with outer secondaries (Figure 5.17a,b,c,d). The loop-forming branches join the superadjacent secondary at an obtuse angle (average 121°) and may form an intramarginal vein in D8605.21Aa&Ba (Figure 5.17b,c), although this is not pronounced. In D8604.39a (Figure 5.17a), however, the loop-forming branches join the superadjacent secondary at a narrow acute angle (average 24°) and are enclosed by secondary and tertiary arches. The tertiary vein combination is AR (Figure 5.17b). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. Tertiary veins form loops outside the secondary loops and marginal ultimate venation appears looped but the feature described as an intramarginal vein may instead represent a fimbrial vein. It appears that specimens D8605.21Aa&Ba (Figure 5.17b,c) may show the position of glands preserved on the lamina, the staining represented by small dark circles in the illustrations.

Differential characters

This morphotype is clearly distinguished from all others with pinnate camptodromous brochidodromous venation within these floras by the course of the secondary veins. The secondaries are recurved or sinuous and are provided with outer secondary veins forming loops (Figure 5.17a,b,c,d).

Discussion

This morphotype appears to be of the first rank (Hickey 1977), with secondary and higher order veins showing an irregular course, intercostal areas that are not uniform in size and shape, and poor differentiation of the tertiary and higher vein orders. The secondary veins are decurrent upon the midvein and the base of the leaf is also decurrent, with poor demarcation of the petiole from the blade. These features are characteristic of modern Magnoliid leaf forms, particularly the Saururaceae, Piperaceae, Aristolochiaceae, and Barclayaceae (Taylor and Hickey 1990). The venation of Morphotype 24 appears similar to that of the Saururaceae and Aristolochiaceae, but leaves of these families usually possess cordate bases.

Taylor and Hickey (1990) described an angiosperm leaf with similar characteristics to Morphotype 24 from the Aptian of Australia. These two leaf forms share an asymmetrical acute decurrent base, prominent midvein, possible pinnate venation with basal pairs which appear to arise from the petiole at an acute angle, irregular brochidodromous secondary veins branching dichotomously to form loops in at least two series and a fimbrial vein. However, this very primitive angiosperm differs from Morphotype 24 in its possession of a multistranded vascular trunk and more disorganised venation and is considered to represent very low first rank. Berry (1938) described a very similar leaf form to Morphotype 24 from the Tertiary of Argentina as *Berberis corymbosifolia*. *B. corymbosifolia* possesses an obovate form, a decurrent base, entire margin and looping secondaries with several orders of loops branching from the exmedial side of the secondary loops. However, the secondary loops in *B. corymbosifolia* appear more elongated parallel to the midvein than those in Morphotype 24.

5.2.26 Morphotype 25

Figure 5.17e,f, Figure 5.18. Plate 2.1C, 3.4C and 3.6A.

Specimen numbers

Hidden Lake Formation: Almost whole leaf: D8754.8.8a&9a (part and counterpart) (excellent). Fragmentary leaf: D8754.8.6b&65a (part and counterpart) (fairly good).

Description

Lamina length 29.4-51.9mm min. Lamina width 17.7-39.8mm min. Using measurements from almost complete specimens, lamina is asymmetrical and ovate (Figure 5.18a,b, Plate 3.6A), with the point of maximum width 37% of the distance from the leaf base. The length/width ratio is 1.66:1. Estimated leaf area 346-1753mm^2 min., microphyllous. Leaf organisation appears simple. Apex is slightly asymmetrical and acute, (apical angle approximately 75°), but the tip

appears blunted, approaching truncate (Figure 5.18a,b). Base is asymmetrical and obtuse normal (Figure 5.18a,b), with a basal angle of approximately 98°. Petiole absent or not preserved. Margin is toothed (Figure 5.18a,b,c,d), indented 0.1-0.8mm, average 0.3mm, approximately 3% of distance to midvein. The largest teeth are at the central part of the leaf margin and the size decreases towards the apex and base of the leaf. The teeth are compound, in two distinct size classes. The average size of the primary teeth is 0.4mm and the secondary teeth, 0.2mm. The primary teeth are fed directly by secondary veins and the secondary teeth are not fed directly by secondary veins. There may also be tertiary teeth, smaller than the others, but these are not clear. Teeth are serrate and average apical angle is obtuse (30-161°, average 100°). However, considering the best preserved primary teeth alone, the average apical angle is acute (77°). Dominant serration type is convex on basal side and convex on apical side. Sinuses are angular or rounded. Tooth spacing is 0.4-3.8mm, average 1.6mm. For each leaf, standard deviation of spacing measurements is 0.7-0.9mm and spacing is described as irregular. Considering the primary teeth only, spacing is 0.7-4.5mm, average 2.3mm, standard deviation 0.9mm, and spacing is still described as irregular.

Venation is pinnate simple craspedodromous (Figure 5.17f, Figure 5.18a,b, Plate 3.6A). At the approximate leaf midpoint, the average primary vein width is approximately 0.71mm wide (range 0.47-0.94mm). The size is approximately 2.67% (range 2.44-2.89%) and is stout (Figure 5.18a). In the almost complete leaf, D8754.8a&9a (Figure 5.18a), the primary vein width tapers from 0.9mm at the base to 0.25mm at the tip. The primary vein course appears to be curved (Figure 5.17f, Figure 5.18a). There are up to 12 opposite or alternate pairs of secondary veins diverging from the midvein at angles of 24-76°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (57°, range 53-61°) (Figure 5.17f, Figure 5.18a,b, Plate 3.4C). Basal secondary veins diverge from midvein at a moderate acute angle (51°) (Figure 5.18a,b). Divergence angle varies irregularly and is symmetrical or asymmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is uniformly curved or recurved and unbranched. There are simple intersecondary veins present (Figure 5.18a). The tertiary vein combination is RR (Figure 5.18a). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an obtuse angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is strongly percurrent (Figure 5.18a). Their course is simple and sinuous or retroflexed. The tertiaries show an oblique relationship to the midvein, the angle decreasing apically. The arrangement is predominantly alternate and they are closely spaced, with at least 6 veins/cm. The higher order venation is not clearly preserved. The secondary and intersecondary veins serving the teeth have a central and direct course. There are no accessory veins visible. Darkened carbon-rich areas may indicate gland position, the discoloration produced by the gland contents. There are darkened areas along the leaf margin, most predominantly in the tooth apices (up to 1mm across), so it appears likely that there may have been some sort of glandular thickening terminating the teeth (Figure 5.18b,c,d, Plate 2.1C). Towards the base of the leaf where the projections are much less prominent and less clear there is again a darkening

along the margin, in some places it appears to be within the smaller projections, but at other points along the basal margin this is less clear. Other fairly extensive darkened regions occur along the midvein and along the secondary veins (Plate 2.1C), perhaps this indicates the position of glands or perhaps the primary and secondary veins were prominent within what was a fleshy leaf (compare Cantrill and Nichols 1996).

Differential characters

This morphotype is distinguished from other morphotypes within these floras by the possession of pinnate simple craspedodromous venation and can be differentiated from others with this type of venation by the right-angled origin of tertiary veins on both the admedial and exmedial sides of the secondary veins, stout midvein and moderate acute divergence of basal secondary veins from the midvein (Figure 5.18a,b, Plate 3.6A). The most obvious differences from other morphotypes are the possible presence of glands in the tooth apices (Figure 5.18b,c,d, Plate 2.1C), the lack of outer secondaries and the presence of intersecondary veins, which all indicate that these leaves should not be included within the Nothofagaceae (Hickey and Wolfe 1975, Zastawniak 1994), unlike Morphotypes 7 and 12.

Discussion

Leaves with pinnate simple craspedodromous venation, percurrent tertiary veins and glandular teeth occur within the Hamamelidae (e.g. Eupteleales, Hamamelidales, Ulmaceae, Moraceae), Dilleniidae (e.g. Dilleniaceae, Actinidiaceae, Saurauiaceae, Aquifoliaceae), and Rosidae (e.g. Rhamnaceae) (Hickey and Wolfe 1975). Since the higher order venation of the teeth is not preserved it is not possible to distinguish between these groups on the basis of tooth type.

Zastawniak (1994) included leaves with simple craspedodromous venation under the Cretaceous Protophyll morphotype (Crabtree 1987). From the Santonian-Maastrichtian of King George Island, Zastawniak (1994) described a leaf form that similar to Morphotype 25 as *Dicotylophyllum* sp. 7. This leaf form possesses similar pinnate venation with subparallel curved secondaries and intersecondary veins, but is very fragmentary with no margins. The leaves of Morphotype 25 show some similarities to *Gnafalea jeffersonii* described by Cantrill and Nichols (1996) from the Albian of Alexander Island with suggested affinities to the Hamamelidae or Dilleniidae. Similarities include a similar form, venation, apical and basal styles, primary vein size, number, course and angle of divergence of secondary veins from the midvein and similarly shaped glandular compound teeth. However, these leaves differ in that the margin of *G. jeffersonii* is described as dentate and shows branching of the secondary veins. Orlando (1964) described a leaf form with a toothed margin and subparallel secondary veins diverging from midvein at a narrow to moderate acute angle as *Tetracera patagonica* (Dilleniaceae) from the Tertiary of King George Island. The features described are similar to those observed in Morphotype 25 and the venation appears to be simple craspedodromous, but the Tertiary leaf form is too poorly preserved for detailed comparison with these Cretaceous leaves.
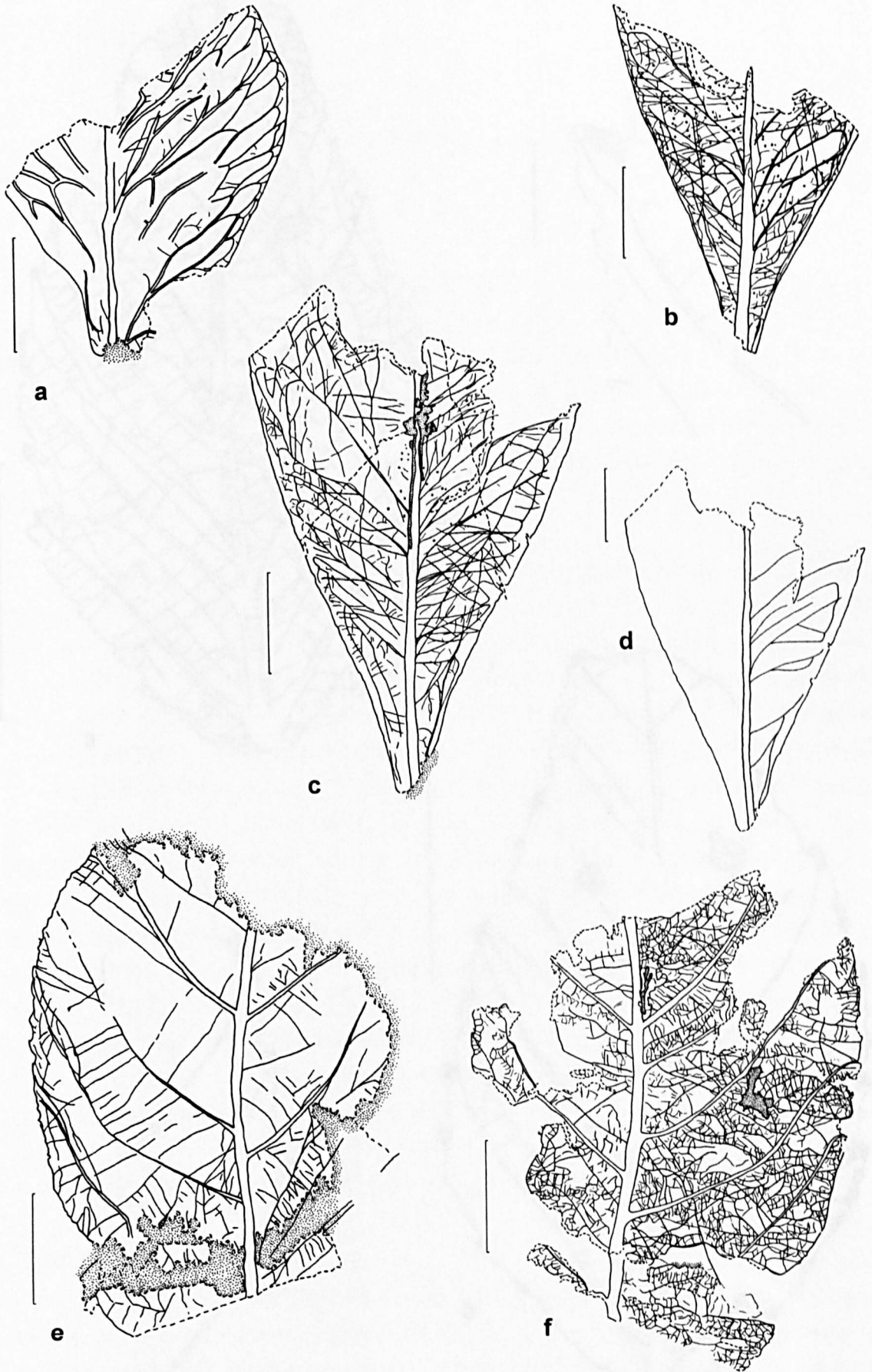
**Figure 5.17 Morphotype 24. (a) D8604.39a. (b) D8605.21Aa. (c) D8605.21Ba.
(d) Simplified drawing of D8605.21Ba.
Morphotype 25. (e) D8754.8.6b. (f) D8754.8.65a.
Scale bar is 10mm.**
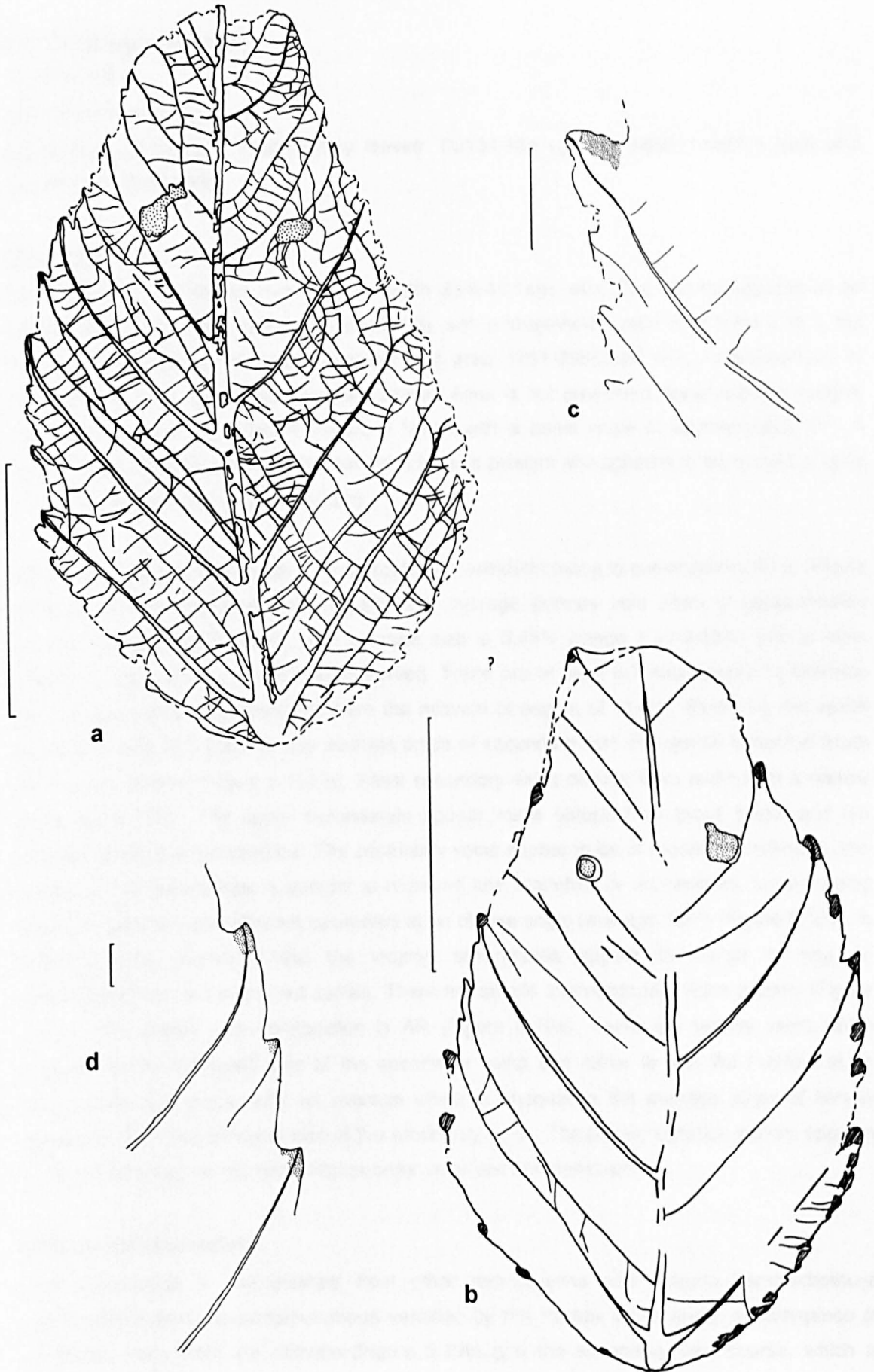
Figure 5.18 Morphotype 25. (a) D8754.8.8a. (b) D8754.8.9a. (c) D8754.8.8a. (d) D8754.8.9a.
Scale bar is 10mm in (a) and (b). Scale bar is 1mm in (c) and (d).

5.2.27 Morphotype 26

Figure 5.19a,b.

Specimen numbers

<u>Santa Marta Formation</u>: Fragmentary leaves: DJ134.16a (good), D8605.1Aa&Ba (part and counterpart) (fairly good).

Description

Lamina length 40.8-98mm min. Lamina width 33.6-41.1mm min. The lamina appears to be roughly symmetrical and oblong (Figure 5.19a), with a length/width ratio of at least 2.38:1, but these are fragmentary leaves. Estimated leaf area 1791-2685mm^2 min., microphyllous to notophyllous. Leaf organisation appears simple. Apex is not preserved. Base appears roughly symmetrical and acute cuneate (Figure 5.19a,b) with a basal angle of approximately 64°. A petiole, approximately 1.6mm wide and 6mm long, is present and appears to be winged (Figure 5.19b). Margin is entire (Figure 5.19a,b).

Venation appears to be pinnate camptodromous brochidodromous to eucamptodromous (Figure 5.19a,b). At the estimated leaf midpoint, the average primary vein width is approximately 1.01mm (range 0.85-1.16mm). The average size is 3.48% (range 3.32-3.63%) and is stout (Figure 5.19a). Primary vein course is curved. There are at least 6-7 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 11-61°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is narrow acute (38°, range 35-40°) (Figure 5.19a,b). Basal secondary veins diverge from midvein at a narrow acute angle (12°). The upper secondaries appear more obtuse than those below and the divergence angle is symmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is straight to recurved and branched or unbranched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 124°) (Figure 5.19a). In D8605.1Aa&Ba (Figure 5.19a) the looping secondaries appear to merge forming an intramarginal vein but this is not certain. There are simple intersecondary veins present (Figure 5.19b). The tertiary vein combination is AR (Figure 5.19a). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern appears to be percurrent but is not clear. Higher order veins are not preserved.

Differential characters

This morphotype is distinguished from other morphotypes with pinnate camptodromous brochidodromous to eucamptodromous venation by the narrow acute angle of divergence of secondary veins from the midvein (Figure 5.19b) and the secondary vein course, which is recurved in parts (Figure 5.19a).

Discussion

Leaves with entire margins and brochidodromous to eucamptodromous venation occur within the Magnoliales, several orders of the Dilleniidae and the Anacardiaceae of the Rosidae (Hickey and Wolfe 1975). The leaves of Morphotype 26 are, however, too fragmentary for detailed comparison with living or fossil forms.

5.2.28 Morphotype 27

Figure 5.19c,d.

Specimen numbers

Santa Marta Formation: Fragmentary leaves: D8605.19Aa (good), D8605.28a (fair).

Description

Lamina length 13-37.3mm min. Lamina width 11.8-13mm min. Lamina appears roughly symmetrical and obovate, with a length/width ratio of at least 2.87:1, but the specimens are too fragmentary for the lamina form to be confidently determined. Estimated leaf area 266-323mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex is not preserved. Base appears to be symmetrical and acute decurrent (Figure 5.19c), with a basal angle of approximately 24°. There appears to be a winged petiole present, approximately 1.6mm wide and 6mm long, but it cannot be clearly distinguished from the lamina. Margin appears to be toothed or erose (Figure 5.19c), indented 0.2-0.4mm, average 0.3mm, approximately 5% of the distance to the midvein. The basal margin is smooth.

Venation appears to be pinnate simple craspedodromous (Figure 5.19c), but since these are fragmentary specimens this may not be an accurate definition. At the estimated leaf midpoint, the average primary vein width is approximately 0.63mm wide (range 0.61-0.65mm). The size is approximately 7.82% (range 7.09-8.55%) and is massive. The primary vein course appears to be straight and unbranched. There are at least 6 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 6-69°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is narrow acute (38°, range 24-51°). Basal secondary veins diverge from midvein at a narrow acute angle (16°). The divergence angle varies irregularly or the upper secondary veins are more obtuse than those below. The divergence is symmetrical. The secondary veins appear relatively fine. The course of the secondaries is straight to recurved and either branched or unbranched. There appears to be simple intersecondary veins present. The tertiary vein combination is AR (Figure 5.19d). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The pattern formed by the tertiary and higher order venation is not clearly preserved.

Differential characters / Discussion

As discussed above, this morphotype is very similar to Morphotype 6. It is distinguished from other morphotypes within the floras by the possession of pinnate simple craspedodromous venation with a petiolate base, massive primary vein and narrow acute angle of secondary divergence from the midvein (Figure 5.19c). Morphotype 27 can be differentiated from Morphotype 6 by the different angles of origin of the tertiary veins. In Morphotype 6 the tertiary vein combination is RA (Figure 5.7d), while in Morphotype 27 the tertiary vein combination is AR (Figure 5.19d). These leaves are, however, too poorly preserved for detailed comparison with other living or fossil angiosperm leaf forms.

5.2.29 Morphotype 28

Figure 5.19e,f,g. Plate 3.9A and 3.10C.

Specimen numbers

<u>Hidden Lake Formation</u>: Fragmentary leaf: D8754.8.48a (fairly good).

<u>Santa Marta Formation</u>: Fragmentary leaf: D8609.147a (fairly good).

Description

Lamina length 24-54.5mm min. Lamina width 9.6-20mm min. The lamina appears to be roughly symmetrical and oblong (Figure 5.19e, Plate 3.10C), with a length/width ratio of about 2.5:1. Estimated leaf area 154-727mm^2 min., microphyllous. Neither the apex nor base is preserved. Margin is entire (Figure 5.19e).

Venation appears to be pinnate camptodromous brochidodromous (Figure 5.19e,f). At the estimated leaf midpoint, the average primary vein width is approximately 0.45mm (range 0.35-0.54mm). The average size is 3.25% (range 2.74-3.76%) and is stout (Figure 5.19e). Primary vein course is curved. There are at least 12 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 30-93°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is moderate acute (54°, range 53-54°) (Figure 5.19e,f). Basal secondary veins are too incompletely preserved for their divergence angle to be accurately measured, but it appears to be narrow acute (average 35°). Divergence angle varies irregularly or the lowest pair of secondaries is more acute than all those above. Secondary vein divergence is symmetrical or asymmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is sinuous, abruptly curved and branched (Figure 5.19e). Loop-forming branches join the superadjacent secondary at an approximate right angle (average 88°). They also appear to be enclosed by secondary, tertiary, or quaternary arches (Figure 5.19e,f). There are composite intersecondary veins present (Figure 5.19e,f). The tertiary vein combination is RA (Figure 5.19f,g). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an acute angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is random reticulate (Figure 5.19e,f,g). The

higher order venation is not clearly preserved but the quaternaries appear relatively randomly oriented (Figure 5.19g). The marginal ultimate venation is looped.

Differential characters

This morphotype can be distinguished from other morphotypes with pinnate camptodromous brochidodromous venation and entire margins by the sinuous to curved course of the secondary veins (Figure 5.19e,f) and the acute angle of origin of tertiary veins on the admedial side of the secondary veins (Figure 5.19g).

Discussion

Leaves with entire margins, pinnate camptodromous brochidodromous venation and random reticulate tertiary veins occur within the Magnoliidae (e.g. Magnoliales, Laurales, Illiciaceae), Hamamelidae (e.g. Balanopales), Caryophyllidae, and Dilleniidae (e.g. Theaceae, Thymelaeales) (Hickey and Wolfe 1975). The basal secondary veins appear to be more acute than the secondaries above, which, along with the presence of intersecondary veins, may indicate that the affinities of Morphotype 28 lie with the Laurales. Since widely disparate leaf groups possess the leaf features observed in Morphotype 28, previous workers have not frequently suggested botanical affinities for leaves of this type from the Antarctic Peninsula.
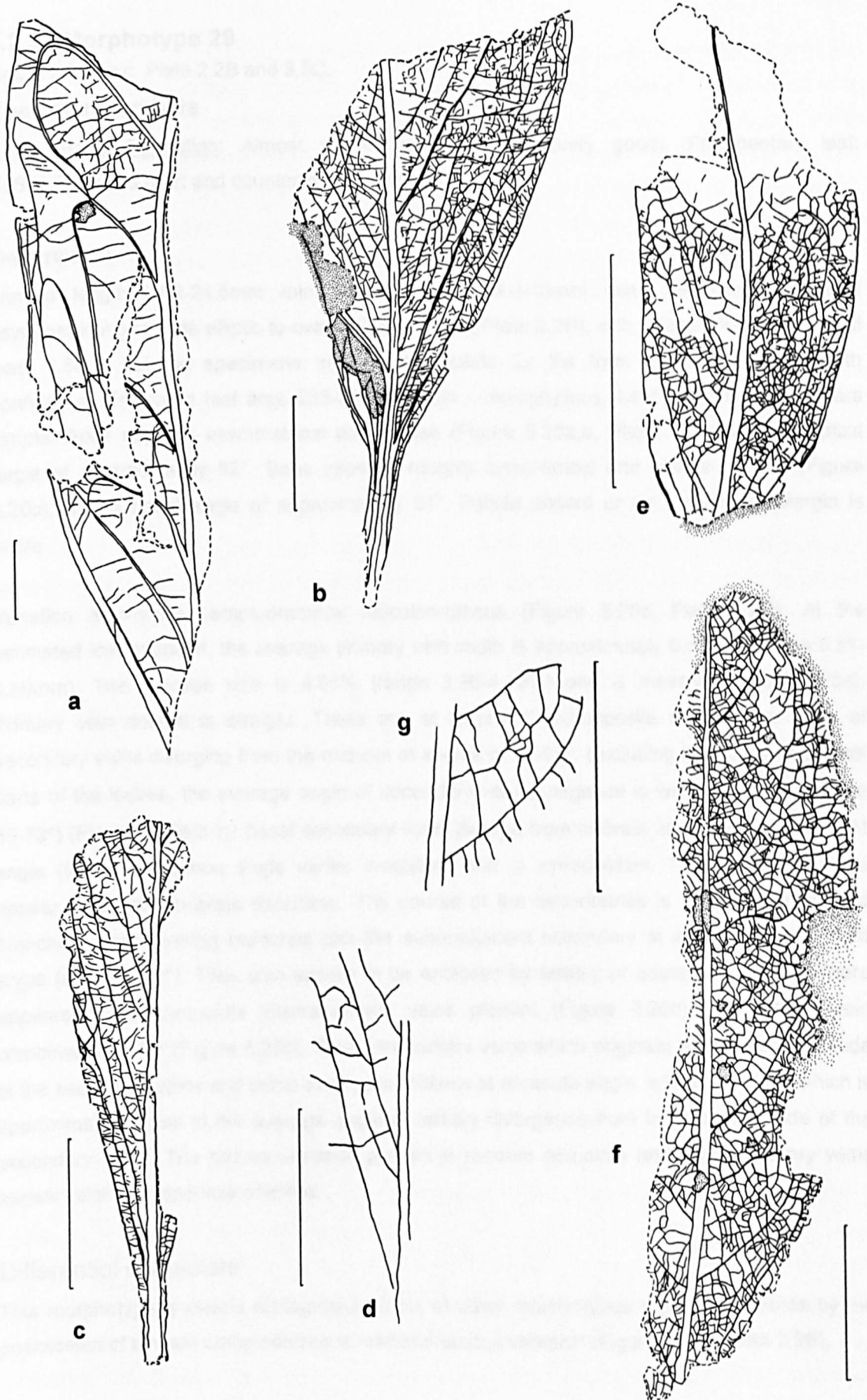
Figure 5.19 Morphotype 26. (a) D8605.1Ba. (b) DJ134.16a.
Morphotype 27. (c) D8605.19Aa. (d) D8605.19Aa.
Morphotype 28. (e) D8609.147a. (f) D8754.8.48a. (g) D8754.8.48a. Scale bar is 10mm.

5.2.30 Morphotype 29

Figure 5.20a,b,c. Plate 2.2B and 3.5C.

Specimen numbers

<u>Santa Marta Formation</u>: Almost whole leaf: DJ147.6a (very good). Fragmentary leaf: D8604.38Aa&Ba (part and counterpart) (very good).

Description

Lamina length 24.2-24.5mm min. Lamina width 14.6-16mm min. The lamina appears asymmetrical and wide elliptic to ovate (Figure 5.20c, Plate 2.2B), with a length/width ratio of at least 1.66:1, but the specimens are too incomplete for the form to be determined with confidence. Estimated leaf area 236-283mm^2 min., microphyllous. Leaf organisation appears simple. Apex appears asymmetrical and obtuse (Figure 5.20a,b, Plate 3.5C), with an apical angle of approximately 92°. Base appears roughly symmetrical and obtuse normal (Figure 5.20c), with a basal angle of approximately 91°. Petiole absent or not preserved. Margin is entire.

Venation is pinnate camptodromous reticulodromous (Figure 5.20c, Plate 2.2B). At the estimated leaf midpoint, the average primary vein width is approximately 0.55mm (range 0.51-0.59mm). The average size is 4.01% (range 3.86-4.15%) and is massive (Figure 5.20c). Primary vein course is straight. There are at least 7-8 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 43-99°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is wide acute (71°, range 69-73°) (Figure 5.20a,b,c). Basal secondary veins diverge from midvein at an approximate right angle (94°). Divergence angle varies irregularly and is symmetrical. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an approximate right angle (average 91°). They also appear to be enclosed by tertiary or quaternary arches. There appears to be composite intersecondary veins present (Figure 5.20c). The tertiary vein combination is AR (Figure 5.20c). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an acute angle, with an average which is approximately equal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is random reticulate and the quaternary veins appear relatively randomly oriented.

Differential characters

This morphotype is clearly distinguished from all other morphotypes within these floras by the possession of pinnate camptodromous reticulodromous venation (Figure 5.20c, Plate 2.2B).

Discussion

This reticulodromous venation, along with an entire margin and random tertiary veins with a tendency towards orientation parallel to the secondary veins (Figure 5.20c) is characteristic of some families of the Ebenales and Ericales (e.g. Ericaceae) (Dilleniidae) (Hickey and Wolfe 1975). Basinger and Christophel (1985) described mummified leaves of the Ebenaceae from the Eocene of Australia, assigning them the name *Austrodiospyros cryptostoma*. The tertiary venation in *A. cryptostoma* is similar to Morphotype 29 in that it is reticulate to percurrent and, in parts of the leaf, shows an almost right-angled relationship to the midvein. Both Morphotype 29 and *A. cryptostoma* possess an entire margin and the shape characteristics of the leaves of Morphotype 29, (wide elliptic to ovate form and obtuse apex and base), are also observed in *A. cryptostoma*. However, *A. cryptostoma* does show a great variability in leaf form. Morphotype 29 and *A. cryptostoma* are differentiated by features of the primary and secondary venation. The venation in *A. cryptostoma* is pinnate camptodromous brochidodromous, rather than reticulodromous as in Morphotype 29. In addition, the primary vein is weaker in *A. cryptostoma* and the divergence of the secondary veins from the midvein is narrow to moderately acute in *A. cryptostoma*, while it is wide acute to approximately right-angled in Morphotype 29. Morphotype 29 is therefore considered dissimilar to these Australian Tertiary leaves. There are no records of forms similar to Morphotype 29 in the Cretaceous floras of the Antarctic Peninsula.

5.2.31 Morphotype 30
Figure 5.20d,e.

Specimen numbers

Santa Marta Formation: Fragmentary leaves: DJ147.56a (good), D8605.24a (fairly good).

Description

Lamina length 12.4-33.1mm min. Lamina width 17.8-19.6mm min. The specimens are too fragmentary for leaf form to be confidently described. Estimated leaf area 357-433mm^2 min., microphyllous. Leaf organisation appears simple. Apex is not preserved. Base is acute normal, with a basal angle of approximately 49°. Petiole is absent or not preserved. Margin is entire (Figure 5.20d).

Venation is pinnate camptodromous brochidodromous (Figure 5.20d). At the estimated leaf midpoint, the primary vein width is approximately 0.23mm. The size is 1.51% max. and is moderate. Primary vein course is curved. There are at least 12 pairs of secondary veins diverging from the midvein at angles of 74-106°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is approximately right-angled (86°) (Figure 5.20d). Basal secondary veins diverge from midvein at a wide acute angle (74°). The lowest pair of secondaries is more acute than all those above. Divergence angle symmetry cannot be assessed for these fragmentary specimens. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 119°). They

also appear to be enclosed by secondary or tertiary arches. There are composite intersecondary veins present. The tertiary vein combination is RR (Figure 5.20d,e). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation appears to be orthogonal reticulate. The higher order venation is distinct and the course of the quaternaries and quinternaries appears to be orthogonal (Figure 5.20e). There is a fimbrial vein present. Quaternary areolation is imperfect, randomly oriented, generally pentagonal and medium sized (0.5-0.9mm).

Differential characters

This morphotype is distinguished from all other leaf morphotypes with pinnate camptodromous brochidodromous venation and entire margins within these floras by the approximately right-angled divergence of the secondary veins from the midvein (Figure 5.20d). In this respect it is similar to Morphotypes 33 and 34, but it is differentiated from these by the possession of a normal acute base, moderate primary vein and tertiary veins with an approximately right-angled origin on the exmedial side of the secondaries.

Discussion

Leaves with entire margins, pinnate camptodromous brochidodromous venation and reticulate tertiary veins occur within the Magnoliidae (e.g. Magnoliales, Laurales) and Dilleniidae (e.g. Theaceae, Thymelaeales) (Hickey and Wolfe 1975).

Birkenmajer and Zastawniak (1989a) recorded the presence of a dicotyledonous leaf with pinnate camptodromous brochidodromous venation and orthogonal reticulate tertiary veins from the Campanian-Maastrichtian of King George Island, but did not name it or suggest possible botanical affinities. Although fragmentary, these leaves can be distinguished by the divergence of the secondary veins, which is much narrower in the King George Island leaf.
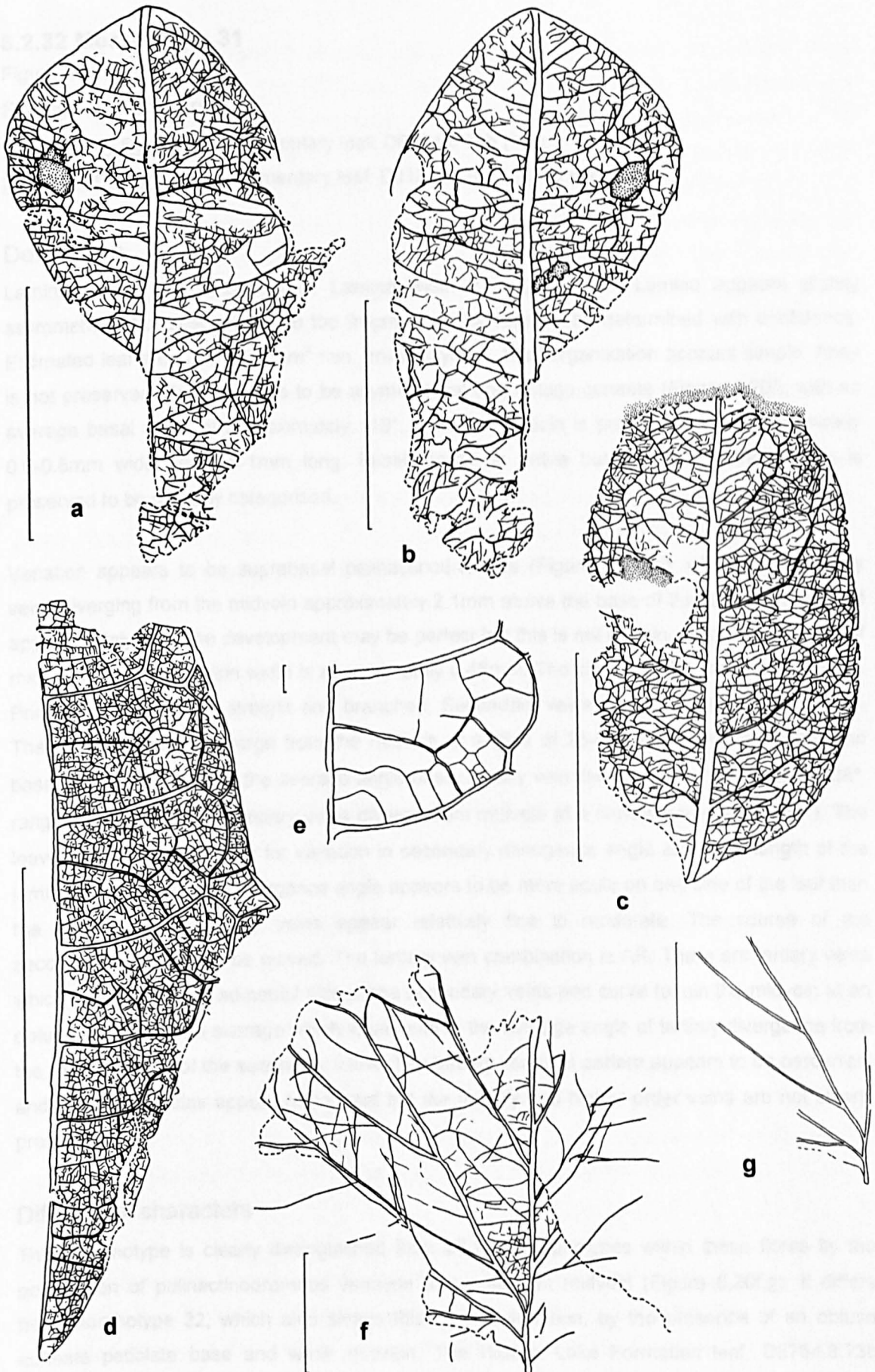
Figure 5.20 Morphotype 29. (a) D8604.38Ba. (b) D8604.38Aa. (c) DJ147.6a.
Morphotype 30. (d) DJ147.56a. (e) DJ147.56a.
Morphotype 31. (f) DJ134.21A/Ba. (g) Simplified drawing of venation in DJ134.21A/Ba.
Scale bar is 10mm in (a), (b), (c), (d), (f) and (g). Scale bar is 1mm in (e).

5.2.32 Morphotype 31

Figure 5.20f,g.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.73b (fair).

Santa Marta Formation: Fragmentary leaf: DJ134.21A/Ba (fairly good).

Description

Lamina length 10.5-35.2mm min. Lamina width 27-47.2mm min. Lamina appears slightly asymmetrical but specimens are too fragmentary for form to be determined with confidence. Estimated leaf area 365-1108mm^2 min., microphyllous. Leaf organisation appears simple. Apex is not preserved. Base appears to be asymmetrical and obtuse cuneate (Figure 5.20f), with an average basal angle of approximately 119°. A normal petiole is present and is approximately 0.6-0.8mm wide and 0.8-1mm long. Basal margin is entire but too little of the margin is preserved to be properly categorised.

Venation appears to be suprabasal palinactinodromous (Figure 5.20f,g), with lateral primary veins diverging from the midvein approximately 2.1mm above the base of the leaf at an angle of approximately 39°. The development may be perfect but this is not certain. At the estimated leaf midpoint, the primary vein width is approximately 0.45mm. The size is 0.95% max. and is weak. Primary vein course is straight and branched. Secondary veins are not clearly distinguished. The secondary veins diverge from the midvein at angles of 25-50°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is narrow acute (38°, range 33-43°). Basal secondary veins diverge from midvein at a narrow acute angle (43°). The leaves are too fragmentary for variation in secondary divergence angle along the length of the lamina to be described. Divergence angle appears to be more acute on one side of the leaf than the other. The secondary veins appear relatively fine to moderate. The course of the secondaries appears to be curved. The tertiary vein combination is AR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an obtuse angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern appears to be percurrent and quaternary veins appear orthogonal but the tertiary and higher order veins are not clearly preserved.

Differential characters

This morphotype is clearly distinguished from all leaf morphotypes within these floras by the possession of palinactinodromous venation and a straight midvein (Figure 5.20f,g). It differs from Morphotype 32, which also shows this type of venation, by the presence of an obtuse cuneate petiolate base and weak midvein. The Hidden Lake Formation leaf, D8754.8.73b (Appendix Volume 2 p140) is just a small fragment and does not represent this morphotype well. This specimen is too poorly preserved for the venation pattern to be categorised and is only included in this morphotype on the basis of the basal form and tertiary vein angles.

Discussion

Leaves with palinactinodromous venation occur within the Hamamelidae (Hickey and Wolfe 1975). Doyle and Hickey (1976) referred to Cretaceous leaves with palinactinodromous venation as 'platanoids', early representatives of the hamamelids now represented by the Platanaceae. One of these 'platanoids', *Protophyllum*, from the Albian-Cenomanian of eastern North America is similar to Morphotype 31. This Northern Hemisphere leaf form is similar to Morphotype 31 in that it is unlobed, possesses palinactinodromous venation with percurrent tertiary veins and is characterised by the nondecurrent junction of the lateral and medial primaries. Cretaceous leaves with this type of venation have been included in the Platanophyll morphotype, with suggested affinities to the Platanales (Crabtree 1987).

Cantrill and Nichols (1996) described a leaf with palinactinodromous venation from the Albian of Alexander Island as *Hydrocotylophyllum alexandri* with suggested affinities to the Chloranthaceae, Saururaceae, Aristolochiaceae or Piperaceae. *H. alexandri* shows primary veins dichotomising over the lamina in a similar fashion to Morphotype 31, but unfortunately this James Ross Island material is too poorly preserved for detailed comparison. However, although both leaf types are petiolate, the petiole of *H. alexandri* is much more prominent than in Morphotype 31.

5.2.33 Morphotype 32

Figure 5.21a,b,c. Plate 3.11A.

Specimen numbers

Hidden Lake Formation: Fragmentary leaves: D8754.8.62a&64a (part and counterpart) (good).

Description

Lamina length 37.1mm min. Lamina width 39.3mm min. Lamina appears to be asymmetrical but since only fragments are present, it is not possible to confidently determine the leaf form. Estimated leaf area 972mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex is not preserved. Base is asymmetrical and obtuse normal (Figure 5.21a), with a basal angle of approximately 99°. Petiole absent or not preserved. The margin appears to be smooth and lobed (Figure 5.21b, Plate 3.11A). There is a clear projection on one side of the leaf. The margin is indented 7.2mm, 36% of the distance to the midvein. Sinus between lobes appears to be angular. The leaf appears to be palmately lobed with three lobes, but these are not clearly preserved (Figure 5.21c).

Venation appears to be basal or possibly suprabasal palinactinodromous (Figure 5.21a,b,c), radiating up to 2.8mm above the leaf base. There are three to possibly five primary veins diverging at angles of 15-46° to the midvein. These may be slightly decurrent. The development appears to be marginal perfect, with primary veins terminating at lobe apices. At the estimated leaf midpoint, the primary vein width is approximately 0.63mm. The size is 1.85% max. and is moderate. Primary vein course is markedly curved. The secondary veins are not clearly

distinguished. There is only one secondary, which appears to be the basal secondary, diverging from the midvein at a wide acute angle (69°). The variation in divergence angle along the length of the lamina and divergence angle symmetry cannot be estimated. The secondary vein appears relatively fine. Its course appears to be curved and unbranched. The tertiary vein combination is AA. There are no clearly preserved tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein. The tertiary venation pattern appears to be percurrent, with convex simple or forked tertiaries trending at approximate right angles to the midvein. They are closely spaced, with approximately 5 veins/cm. The quaternary veins may have an orthogonal course but the venation is too poorly preserved for this to be confirmed. The irregularly percurrent tertiary veins may indicate that Morphotype 32 is of the third rank, but the specimens are too poorly preserved for this to be confidently ascertained (Figure 5.21b).

Differential characters

This morphotype is clearly distinguished from all leaf morphotypes within these floras by the possession of palinactinodromous venation and a lobed margin (Figure 5.21a,b,c, Plate 3.11A). It is also differentiated from Morphotype 31, which also shows this type of venation, by the presence of an obtuse normal base and a moderate curved midvein.

Discussion

The discussion of Morphotype 31 above outlines the assignment of Cretaceous leaves with palinactinodromous venation to the Platanales, but some lobed leaves with palinactinodromous venation have been grouped under the Pentalobaphyll (Araliaphyll) morphotype, with possible affinities to the Laurales or Rosidae (Crabtree 1987). Morphotype 32 is considered most similar to the Pentalobaphylls because these forms possess a smooth lobed margin, three primary veins diverging from the leaf base with two veins branching from the lateral primaries, weakly developed possibly eucamptodromous secondary veins and percurrent tertiaries. Upchurch *et al.* (1994) outlined five venation features that may be used to establish resemblance of Cretaceous leaves with palinactinodromous venation to the Laurales. These features include an initial point of primary vein divergence at the leaf base, recurved lateral primaries, relatively thin secondary and tertiary veins compared with the 'platanoids' and darkening of the margin near the leaf base suggesting the presence of a fimbrial vein. These characteristics are present in Morphotype 32, but the fifth venational feature indicating lauralean affinities relates to external branches of the lateral primaries, which are not preserved in Morphotype 32. Using these criteria, Upchurch *et al.* (1994) suggested that the leaves recorded as *Araliaephyllum obtusilobum* from the Albian of eastern North America were lauralean. Similarities between *A. obtusilobum* and Morphotype 32 include a palmately lobed margin, palinactinodromous venation, thin irregularly percurrent tertiaries between the primaries and possible third rank. However, the looping secondaries present in *A. obtusilobum* are not visible in Morphotype 32.

Zastawniak (1994) described two leaf fragments with palinactinodromous venation from the Santonian-Maastrichtian of King George Island. These were included under the Pentalobaphyll (Araliaephyll) morphotype and named *Dicotylophyllum* sp. 4. Zastawniak (1994) described these

leaves as having three primary veins with lateral primary veins probably branching off from the lateral primaries above the base and suggested affinities to the Dilleniidae, but these King George Island specimens are too poorly preserved for more detailed comparison with Morphotype 32. Cantrill and Nichols (1996) described a leaf form with palinactinodromous venation from the Albian of Alexander Island, assigning it to *Araliaphyllum quinquelobatus* and suggesting that it showed affinities to the Laurales. This palmate leaf form is very similar to Morphotype 32, with 3-5 smooth margined lobes, 3-5 weakly decurrent recurved primaries, diverging at a similar angle to the midvein. Other similarities include the termination of the primary veins in the lobe apices and the angle of divergence of the secondary veins, which do not reach the leaf margin, but the brochidodromous loops observed in *A. quinquelobatus* are not present in Morphotype 32. The sinus bracing by secondary veins described for *A. quinquelobatus* is also not preserved in the fragmentary James Ross Island leaf. Despite these differences, it is considered that Morphotype 32 possesses sufficient diagnostic characters to suggest an affinity with the Laurales.

5.2.34 Morphotype 33
Figure 5.21d.

Specimen numbers

Santa Marta Formation: Almost whole leaf: DJ147.14a (good). Fragmentary leaf: DJ147.17a (fairly good).

Description

Lamina length 34.4-39mm min. Lamina width 17.2-19.4mm min. The lamina is asymmetrical and oblong, with a length/width ratio of about 2:1. Estimated leaf area 395-504mm^2 min., microphyllous. Apex is asymmetrical and acute, with an apical angle of approximately 55°. Base is not preserved. Margin is entire (Figure 5.21d).

Venation is pinnate camptodromous brochidodromous (Figure 5.21d). At the estimated leaf midpoint, the average primary vein width is approximately 0.31mm (range 0.24-0.38mm). The average size is 2.09% (range 1.38-2.79%) and is stout. Primary vein course is curved. There are at least 12 subopposite to alternate pairs of secondary veins diverging from the midvein at angles of 50-100°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is approximately right-angled (84°, range 82-85°). Basal secondary veins are not preserved. Divergence angle appears nearly uniform and is symmetrical in the most complete specimen. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an approximate right angle (average 98°). They also appear to be enclosed by secondary, tertiary or quaternary arches. There appears to be simple intersecondary veins present. The tertiary vein combination is AR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary

divergence from the exmedial side of the secondary veins. The tertiary venation pattern is not clearly preserved and the higher order venation cannot be clearly determined, but the marginal ultimate venation is looped.

Differential characters

This morphotype is separated from other morphotypes with pinnate camptodromous brochidodromous venation and entire margins within these floras by the possession of an oblong form, acute apex, stout primary vein and curved secondary veins diverging from the midvein at an approximate right angle (Figure 5.21d). In addition the acute angle of origin of the tertiary veins on the exmedial side of the secondary veins is not observed in many of the entire margined morphotypes with this type of venation. However, Morphotype 33 and Morphotype 34 are very similar and it is possible that with more complete preservation they may have been included within the same morphotype.

Discussion

Leaves with pinnate camptodromous brochidodromous venation and entire margins occur within the Magnoliidae (e.g. Magnoliales, Laurales, Illiciaceae), Hamamelidae (e.g. Balanopales), Caryophyllidae, Dilleniidae (e.g. Sapotaceae, Primulales), and the Rosidae (e.g. Fabales) (Hickey and Wolfe 1975). This Cretaceous leaf form is too incompletely preserved for close comparison with living or fossil angiosperm leaves.

5.2.35 Morphotype 34

Figure 5.21e. Plate 3.11E.

Specimen numbers

Hidden Lake Formation: Almost whole leaf: D8754.8.39a (excellent).

Description

Lamina length 21.8mm. Lamina width 8.2mm. Whole lamina is roughly symmetrical and narrow ovate (Figure 5.21e, Plate 3.11E), with the point of maximum width at 33% of the distance from the leaf base. The length/width ratio is 2.66:1. Leaf area 119mm^2 min., microphyllous. Leaf organisation appears simple. Apical angle approximately 52°. Apex originally described as long acuminate because of the concave margins observed in upper left hand side of D8754.8.39a (Figure 5.21e), but the margin is only slightly concave so the apex may be more accurately described as attenuate. Basal angle is approximately 82° and base is rounded. Petiole is absent or not preserved. Margin is entire.

Venation is pinnate camptodromous brochidodromous (Figure 5.21e). At the estimated leaf midpoint, the primary vein width is approximately 0.26mm. The size is 3.38% and is stout. Primary vein course is curved. There are approximately 12 opposite or alternate pairs of secondary veins diverging from the midvein at angles of 51-120°. Excluding the apical and basal parts of the leaf, the average angle of secondary vein divergence is approximately right-

angled (84°). Basal secondary veins diverge from midvein at a wide acute angle (69°). Divergence angle varies irregularly and is more acute on one side of the leaf than the other. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and unbranched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 104°). They also appear to be enclosed by tertiary or quaternary arches. There may be simple intersecondary veins present but this is not clear. The tertiary vein combination is AR. There are no clearly preserved tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein. The tertiary venation pattern is not preserved.

Differential characters

This leaf is clearly distinguished from others with pinnate camptodromous brochidodromous venation within these floras by its symmetrical lamina and rounded base (Figure 5.21e, Plate 3.11E).

Discussion

As stated in the discussion of Morphotype 33, Morphotype 34 is very similar to Morphotype 33 and shares possible affinities with the Magnoliidae, Hamamelidae, Caryophyllidae, Dilleniidae and Rosidae (Hickey and Wolfe 1975). However, Morphotype 34 possesses several features which are characteristic of many genera of the Annonaceae (e.g. *Cyathostemma*, *Miliusa*, *Duguetia*, *Uvaria*, *Guatteria*, *Anaxagorea*, *Haplostichanthus*) (Klucking 1986, Christophel and Hyland 1993). For example, *Cyathostemma micranthum* shares with Morphotype 34 an ovate form, similarly shaped apex, rounded base, entire margin, pinnate camptodromous brochidodromous venation, curved primary vein and 10-15 opposite or alternate secondary veins diverging from the midvein irregularly at a wide acute to approximate right angle. The loop forming branches join the superadjacent secondary at an obtuse angle and secondary loops are enclosed by tertiary and quaternary arches showing a similar pattern to Morphotype 34. However, these characteristics are also seen in other Magnoliid families such as the Monimiaceae (e.g. *Leiveria*). Unfortunately the intercostal and higher order venation is not preserved in Morphotype 34, preventing further comparison.
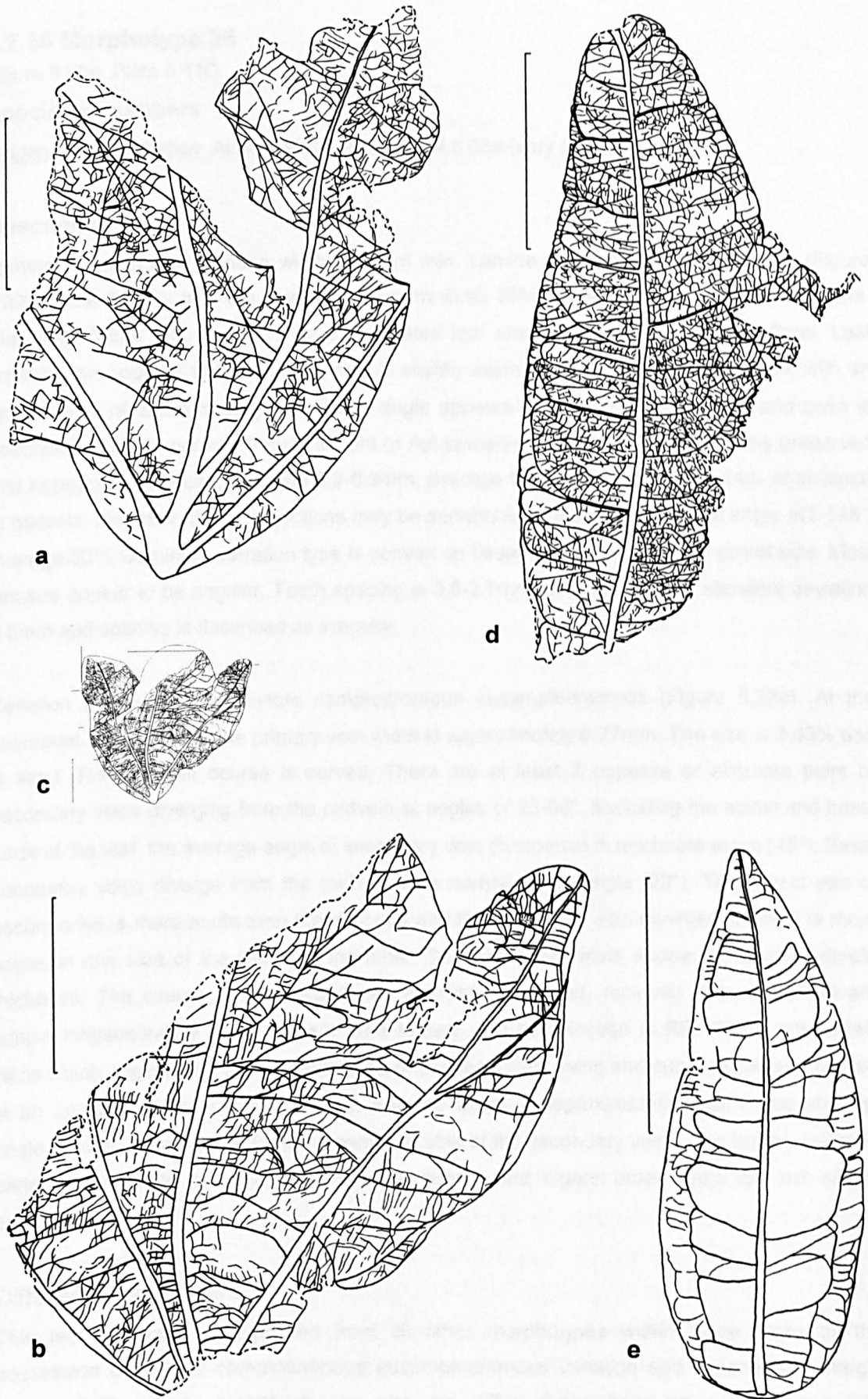
Figure 5.21 Morphotype 32. (a) D8754.8.64a. (b) D8754.8.62a.
(c) D8754.8.62a&64a. Morphotype 33. (d) DJ147.14a.
Morphotype 34. (e) D8754.8.39a. Scale bar is 10mm.

5.2.36 Morphotype 35

Figure 5.22a. Plate 3.11D.

Specimen numbers

Hidden Lake Formation: Almost whole leaf: D8754.8.63a (very good).

Description

Lamina length 52mm. Lamina width 26.3mm min. Lamina is asymmetrical and ovate (Figure 5.22a, Plate 3.11D), with the point of maximum width 36% of the distance from the leaf base. The length/width ratio is 1.98:1 max. Estimated leaf area 912mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex is slightly asymmetrical and long acuminate, with an apical angle of approximately 45°. Basal angle appears to be approximately 88° and base is described as acute normal. Petiole absent or not preserved. Margin is not completely preserved and appears to be erose, indented 0.2-0.9mm, average 0.4mm, approximately 14% of distance to midvein. However, these projections may be serrations, with an obtuse apical angle (41-148°, average 93°). Dominant serration type is convex on basal side and straight on apical side. Most sinuses appear to be angular. Tooth spacing is 0.8-2.7mm, average 1.7mm, standard deviation 0.5mm and spacing is described as irregular.

Venation appears to be pinnate camptodromous eucamptodromous (Figure 5.22a). At the estimated leaf midpoint, the primary vein width is approximately 0.77mm. The size is 3.63% and is stout. Primary vein course is curved. There are at least 7 opposite or alternate pairs of secondary veins diverging from the midvein at angles of 23-68°. Excluding the apical and basal parts of the leaf, the average angle of secondary vein divergence is moderate acute (46°). Basal secondary veins diverge from the midvein at a narrow acute angle (23°). The lowest pair of secondaries is more acute than those above and the secondary vein divergence angle is more acute on one side of the leaf than the other. The secondary veins appear to be of moderate thickness. The course of the secondaries is uniformly curved, recurved in parts. There are simple intersecondary veins present. The tertiary vein combination is RR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is approximately equal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern appears to be percurrent, but the tertiary and higher order veins are not clearly preserved.

Differential characters

This leaf is clearly distinguished from all other morphotypes within these floras by the possession of pinnate camptodromous eucamptodromous venation and a non-entire margin (Figure 5.22a, Plate 3.11D). It can also be differentiated from other leaf types with eucamptodromous venation by the moderate acute divergence of recurved secondary veins from the midvein, with the basal pair of secondaries more acute than all those above.

Discussion

Leaves with eucamptodromous venation and toothed margins (Figure 5.22a) occur within the Dilleniidae, e.g. some Ebenales and some Celastrales (Hickey and Wolfe 1975), although the Celastrales were included in the Rosidae by Cronquist (1981). There have been no similar leaf forms recorded from the Cretaceous of the Antarctic Peninsula.

5.2.37 Morphotype 36

Figure 5.22b,c. Plate 3.4D.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.43a (very good).

Description

Lamina length 33mm min. Lamina width 16mm. Lamina appears slightly asymmetrical and elliptic to narrow obovate (Figure 5.22b, Plate 3.4D), with a length/width ratio of at least 2.06:1. Estimated leaf area 352mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex is not preserved. Base is roughly symmetrical and acute and cuneate (Figure 5.22b), with a basal angle of approximately 71°. Petiole absent or not preserved. Margin is toothed (Figure 5.22b,c), indented 0.2-0.5mm, average 0.3mm, approximately 4% of the distance to the midvein. Teeth are simple, serrate and average apical angle is acute (42-82°, average 67°). Dominant serration type is acuminate on basal side and convex on apical side. Most of the sinuses appear to be angular. Tooth spacing is 3.1-5.3mm, average 4mm, standard deviation 0.9mm and spacing is described as regular.

Venation appears to be pinnate camptodromous brochidodromous (Figure 5.22b). At the estimated leaf midpoint, the primary vein width is approximately 0.27mm. The size is 1.75% and is moderate. Primary vein course is straight. There are at least 6 alternate pairs of secondary veins diverging from the midvein at angles of 14-61°. Excluding the apical and basal parts of the leaf, the average angle of secondary vein divergence is moderate acute (49°) (Figure 5.22b). Basal secondary veins diverge from midvein at a narrow acute angle (18°). The lowest pair of secondaries is more acute than all those above and the secondary vein divergence is more acute on one side of the leaf than the other. The secondary veins appear to be of moderate thickness. The course of the secondaries is sinuous and abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an approximate right angle (average 94°). They also appear to be enclosed by secondary, tertiary or quaternary arches. The tertiary vein combination is OA. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an acute angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is orthogonal reticulate to weakly percurrent (Figure 5.22b). The quaternary veins appear relatively randomly oriented but are not clearly distinguished. There is a concentration of dark material in the tooth apices that may suggest the presence of

glands. The principal vein of the tooth appears to be a deflected tertiary showing an eccentric course (Figure 5.22c).

Differential characters

This leaf is clearly distinguished from other leaf morphotypes with pinnate camptodromous brochidodromous venation within these floras because it is the only one with a toothed margin (Figure 5.22b,c). It can also be differentiated by the obtuse angle of tertiary vein origin on the exmedial side of the secondary veins.

Discussion

Leaves with pinnate camptodromous brochidodromous venation occur within the Laurales (Magnoliidae) and the Dilleniidae (e.g. Ericales, Ebenales, Celastrales, Theaceae) (Hickey and Wolfe 1975). There are leaf forms within both the Laurales (e.g. *Daphnandra*, Atherospermataceae) and the Dilleniidae (e.g. *Maytenus*, Celastraceae) with a similar form, basal style, toothed margin, and brochidodromous secondary veins diverging from the midvein at a moderate acute angle, with the basal pair decurrent and more acute than those above. The average angle of origin of the exmedial tertiaries in Morphotype 36 is obtuse, which also appears to be the case for *Maytenus*, while species of *Daphnandra* frequently show tertiary veins arising from the exmedial side of secondary veins at a more acute angle. However, there are also some species of *Daphnandra*, such as *D. micrantha*, which also show exmedial tertiary veins arising at a more obtuse angle. It is also difficult to choose between one or the other of these two major plant groups as the most similar to Morphotype 36 based on tooth type because both groups possess leaves with glandular teeth. However, the acuminate-convex acute shape of the teeth observed in Morphotype 36 is characteristic of the monimioid tooth type present in certain families of the Laurales.

Cantrill and Nichols (1996) described a leaf form with brochidodromous venation and a toothed margin from the Albian of Alexander Island as *Ficophyllum palustris* with suggested affinities to the Magnoliales. However, the base of *F. palustris* is rounded, the divergence of the secondary veins shows a different pattern to Morphotype 36 and the teeth are different shape, with no evidence of glands. Dusén (1908) illustrated a leaf with possible affinities to the Aquifoliaceae (Celastrales), *Iliciphyllum* sp. 1. This leaf form appears to have brochidodromous venation and a serrate margin with a similar form, basal style, and secondary and tertiary venation pattern to Morphotype 36. However, the secondary veins diverge at different angles and the tooth shape is different.

Birkenmajer and Zastawniak (1989a) described a leaf form from the Tertiary of King George Island as *Monimiophyllum antarcticum* (including a dicotyledonous leaf illustrated by Czajkowski and Rösler 1986) with suggested affinities to the Monimiaceae. This leaf possesses monimioid teeth and irregularly spaced sinuous secondary veins forming loops. However, this Tertiary leaf form differs from Morphotype 36 because *M. antarcticum* has a different form, rounded sinuses, semicraspedodromous venation, secondary veins diverging from the midvein at a wide acute

angle and random reticulate tertiary venation. Dusén (1908) assigned a leaf from the Tertiary of Seymour Island to *Laurelia insularis* with suggested affinities to the Atherospermataceae. This leaf is similar to Morphotype 36 in that it appears to have a serrate margin and brochidodromous venation, but the secondary vein angles are different and the teeth are a different shape and larger with respect to the size of the leaf in the Tertiary material. Orlando (1964) also illustrated a leaf assigned to *Laurelia insularis* from the Tertiary of King George Island. The poor preservation of this leaf form does not allow clear comparison with Morphotype 36. The leaf form described as *Laurelia guiñazui* by Berry (1938) from the Tertiary of Argentina is also similar to Morphotype 36. *L. guiñazui* has an elliptic form, cuneate base, and margin with glandular serrations similar to Morphotype 36. From the illustration, the Argentine material also appears to show similar venation to Morphotype 36. *L. guiñazui* possesses ascending brochidodromous venation, with six or seven secondaries diverging from the midvein at a moderate acute angle, loop-forming branches joining the superadjacent secondary at an approximate right angle, and tertiary veins supplying the teeth. The tertiary venation pattern in *L. guiñazui* may also be orthogonal reticulate, but the preservation of the Tertiary leaves does not allow more detailed comparison with Morphotype 36. There is support for the occurrence of Atherospermataceae on the Late Cretaceous Antarctic Peninsula from fossil wood described as *Laurelites jamesrossii* by Poole and Francis (1999) from slightly younger Santonian strata.

5.2.38 Morphotype 37
Figure 5.22d,e,f,g.
Specimen numbers
Santa Marta Formation: Fragmentary leaf: DJ147.49Aa&Ba (part and counterpart) (good).

Description
Lamina length 25.8mm min. Lamina width 48.8mm min. Lamina is fragmentary but it appears to be ovate (Figure 5.22d,e,f,g). Estimated leaf area 839mm^2 min., microphyllous. Leaf organisation appears to be simple. Apex is not preserved. Basal angle is estimated to be 167° and base is described as hastate (Figure 5.22e,g). There appears to be a normal petiole present, approximately 1.7mm wide and 1.7mm long. Margin is lobed (Figure 5.22d,e), indented at least 7.5mm, approximately 38% of distance to midvein. The sinus preserved appears quite angular. Spacing between lobes is about 17.3mm, but the lobes are incomplete. The margin of the lobes also appears to be crenate.

Venation is basal marginal actinodromous (Figure 5.22d,e,g), with two lateral primary veins diverging from the leaf base at an angle of 57° to the midvein. The development appears to be imperfect but the leaf is too fragmentary for confident assessment of the development. At the estimated leaf midpoint, the primary vein width is approximately 0.52mm. The size is 1.11% max. and is weak. Primary vein course is straight. There is only one pair of opposite secondary veins preserved diverging from the midvein at angles of 42-52°. Excluding the apical and basal parts of the leaf, the average angle of secondary vein divergence is moderate acute (48°), and

these are the basal secondary veins. The variation in divergence angle along the length of the lamina cannot be assessed from these fragmentary specimens. The divergence angle is more acute on one side of the leaf than the other. The secondary veins are moderate to relatively thick. The course of the secondaries appears to be straight and unbranched. The tertiary vein combination is AR (Figure 5.22d,e). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern is weakly percurrent, with forked tertiaries trending at an obtuse angle to the midvein. Their arrangement is predominantly alternate and they are closely spaced, with at least 4 veins/cm. Within the lobes, the tertiary veins form loops. The course of the quaternary veins appears orthogonal.

Differential characters

Though fragmentary, this leaf is clearly different to all the other morphotypes within these floras because it possesses actinodromous venation, a non-entire lobed margin and a hastate base (Figure 5.22d,e,g).

Discussion

As stated in the discussion of Morphotype 2, the actinodromous venation and weakly percurrent tertiaries concentrically oriented with respect to the top of the petiole (Figure 5.22d,e) is characteristic of the Dilleniidae (Hickey and Wolfe 1975). There are several genera within the Sterculiaceae, such as *Fremontia*, *Sterculia* and *Ruizia*, which show very similar features to Morphotype 37. Similarities include an ovate form, hastate base, non-entire lobed margin, basal marginal actinodromous venation, and tertiary veins that are weakly percurrent in the intercostal areas, forming loops in the lobe apices. *Ruiza* also possesses secondary veins that terminate in the centre of lobe apices.

Berry (1937c) described lobed leaves with actinodromous venation from the Late Cretaceous of Patagonia as *Sterculia sehuensis*. This leaf form is similar to Morphotype 37 in that it possesses three stout primaries diverging from the base, but the lobes extend more than 50% of the distance to the base and the lobe margins are smooth in *S. sehuensis*. Birkenmajer and Zastawniak (1989a) described leaves from the Late Cretaceous-early Tertiary of King George Island and Dufayel Island as *Dicotylophyllum latitrilobatum*, with possible affinities to the Hamamelidae or Dilleniidae, and in particular *Cochlospermum or Sterculia*. They also included other records from the Late Cretaceous and Tertiary of the Antarctic Peninsula within this species, including *Phyllites* sp. 9 (Dusén 1908), an undetermined dicotyledonous leaf (Barton 1964), ?*Sterculia* (Birkenmajer and Zastawniak 1986), and *Sterculia* cf. *S. washburnii* (Czajkowski and Rösler 1986). This leaf form possesses basal marginal actinodromous venation, but differs from Morphotype 37 because the lobe margins are smooth, the base is obtuse, the secondary veins are brochidodromous and the tertiaries are random reticulate in *D. latitrilobatum*.
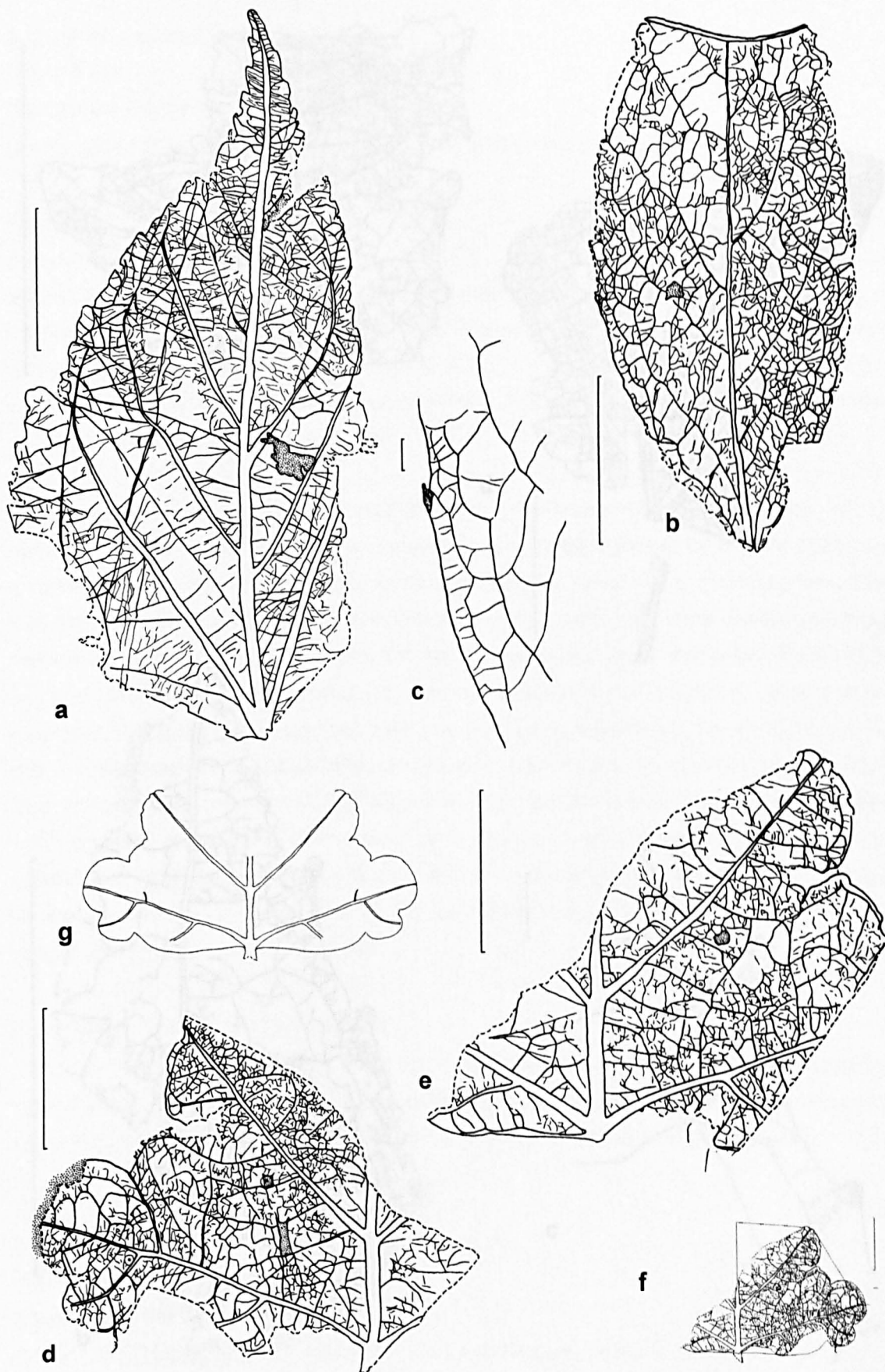
Figure 5.22 Morphotype 35. (a) D8754.8.63a.
Morphotype 36. (b) D8754.8.43a. (c) D8754.8.43a.
Morphotype 37. (d) DJ147.49Ba. (e) DJ147.49Aa. (f) DJ147.49Aa&Ba.
(g) Interpretative diagrammatic sketch of the form and venation of Morphotype 37.
Scale bar is 10mm in (a),(b),(d),(e) and (f). Scale bar is 1mm in (c).

5.2.39 Morphotype

Figure 5.23a

Specimen number

Pollen Lake Flora...

Description

Lamina ... The leaf appear ... form, ... the large apices of ... blade, approximately half of the distance to the nearest secondary ... Crenation spacing is estimated to be at least 6 mm.

Venation appears to be pinnate camptodromous brochidodromous (Figure 5.23a). At the estimated leaf midpoint, the primary vein width is approximately 0.6 mm. The size is 1 mm and is moderate. Primary vein course appears to be straight but this is only a small fragment of the leaf. There are at least three opposite or alternate pairs of secondary veins diverging from the midvein at angles of 40-75°. Excluding the apical and basal portions of the leaves, the average angle of secondary vein divergence is wide acute (71°). Basal secondary veins are not preserved. The angle of angle appears nearly uniform and symmetrical in this small part of the leaf. The secondary ... appear to be of moderate thickness. The course of the secondaries is abruptly curved up brochidate. The tertiary vein chloridodal is AO. There are tertiary veins which originate on the upper side of the secondary ... and loop toward the midvein at an approximate ... average which is superior to the internal angle of tertiary alternate ... from the lower side of the secondary veins. The tertiary and higher order venation is not well-preserved ... leaf.

Comparison, Discussion / Identification

The leaf ... all other specimens with pinnate camptodromous brochidodromous ... the nature of its crenate margin (right hand side of Figure 5.23a) ... for its detailed structure to be ...

5.2.40 Morpho...

Figure 5.23b,c; ...

Specimen number

Pollen Lake Flora ... elementary leaf. D8754.8.34b (early poor)

Description

Lamina length 16.8 mm ... is a fragment from the apical part of the leaf ... diameter 1 mm; angle

Figure 5.23 Morphotype 38. (a) D8754.8.22b.
Morphotype 39. (b) D8754.8.34b. (c) D8754.8.34b.
Morphotype 40. (d) DJ147.45a.
Scale bar is 10mm in (a),(b) and (d). Scale bar is 1mm in (c).

5.2.39 Morphotype 38

Figure 5.23a.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.22b (fairly good).

Description

Lamina length 10.9mm min. Lamina width 13.2mm min. The parts of the lamina preserved appear symmetrical but the leaf is too fragmentary to confidently determine lamina form. Estimated leaf area 96mm² min., microphyllous. Neither the apex nor base is preserved. Margin appears crenate (right hand side of Figure 5.23a), indented 0.4-1.4mm, average 0.9mm, approximately 14% of the distance to the midvein. Sinuses appear to be angular. Crenation spacing is estimated to be at least 3.6mm.

Venation appears to be pinnate camptodromous brochidodromous (Figure 5.23a). At the estimated leaf midpoint, the primary vein width is approximately 0.59mm. The size is 4.68% and is moderate. Primary vein course appears to be straight but this is only a small fragment of the leaf. There are at least three opposite or alternate pairs of secondary veins diverging from the midvein at angles of 69-73°. Excluding the apical and basal parts of the leaves, the average angle of secondary vein divergence is wide acute (71°). Basal secondary veins are not preserved. Divergence angle appears nearly uniform and symmetrical in this small part of the leaf. The secondary veins appear to be of moderate thickness. The course of the secondaries is abruptly curved and unbranched. The tertiary vein combination is AR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary and higher order venation pattern is not clearly preserved.

Differential characters / Discussion

This leaf is clearly distinguished from all other specimens with pinnate camptodromous brochidodromous venation in these floras by the nature of its crenate margin (right hand side of Figure 5.23a). However, it is too fragmentary for its botanical affinities to be determined.

5.2.40 Morphotype 39

Figure 5.23b,c. Plate 3.10A.

Specimen numbers

Hidden Lake Formation: Fragmentary leaf: D8754.8.34b (fairly good).

Description

Lamina length 16.8mm min. Lamina width 12.2mm min. The specimen is a fragment from the apical part of the leaf only so the lamina form cannot be determined. Estimated leaf area

137mm² min., microphyllous. Apex appears to be acute (Figure 5.23b), with an apical angle of approximately 54°. Base is not preserved. Margin is non-entire (Figure 5.23b,c, Plate 3.10A), indented 0.7mm, approximately 15% of distance to midvein. The projections have rounded apices so they are described as crenations. Sinuses appear rounded and crenation spacing is approximately 3.8mm.

Venation appears to be pinnate semicraspedodromous (Figure 5.23b,c) but the leaf is too fragmentary for confident assessment of venation type. At the estimated leaf midpoint, the primary vein width is approximately 0.15mm. The size is 1.6% and is moderate. Primary vein course appears to be curved. There are at least 6 alternate pairs of secondary veins diverging from the midvein at angles of 68-118°. Excluding the apical part of the leaf, the average angle of secondary vein divergence is approximately right-angled (88°) (Figure 5.23b). Basal secondary veins are not preserved. The secondary vein divergence angle appears to vary irregularly and is more acute on one side of the leaf than the other. The secondary veins appear relatively fine. The course of the secondaries is sinuous, abruptly curved and branched. Loop-forming branches join the superadjacent secondary at an obtuse angle (average 106°). There may be simple intersecondary veins present but this is not clear. The tertiary vein combination is RR (Figure 5.23b). There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern appears to be weakly percurrent. The higher order venation is not clearly preserved. There are dark concentrations in the apices of the marginal projections, which may reflect gland position. The crenations are served by tertiary veins following an eccentric, deflected course (Figure 5.23b,c).

Differential characters

This morphotype is distinguished from other morphotypes within these floras by the presence of pinnate semicraspedodromous venation, a non-entire margin and the secondary vein pattern. The margin of Morphotype 39 (Figure 5.23b,c) is described as crenate because the apices of the projections are rounded rather than pointed. However, these projections may better be described as glandular teeth. The venation pattern and tooth characteristics of Morphotype 39 are very similar to those of Morphotype 4. If the leaf representing Morphotype 39 had been more completely preserved it may have been included within Morphotype 4, but this fragmentary leaf has been kept separate at this stage on the basis of the approximately right-angled divergence of sinuous secondary veins forming 'square' loops.

Discussion

The teeth of Morphotype 39 (Figure 5.23b,c) are described as cunonioid, with glandular apices and with the principal vein to each tooth branching below it, sending one branch to the superadjacent secondary vein and the other to the tooth apex along its apical side (Hickey and Wolfe 1975). As discussed for Morphotype 4, cunonioid teeth, along with semicraspedodromous venation and percurrent tertiaries, are characteristic of Rosid orders such as the Saxifragales,

Sapindales, Rhamnales (Leeaceae) and Oleales. Figure 5.24b illustrates the tooth architecture of extant Cunoniaceae (*Ackama rosafolia*) drawn from herbarium material. This drawing shows teeth with a similar shape to Morphotype 39 with deflected veins running along the apical side of the teeth. The tertiary venation pattern observed in *A. rosafolia* is also very similar to that of Morphotype 39. The glandular tooth apices with secondary veins that bifurcate near the tooth, one branch entering the tooth and the other joining the adjacent secondary vein, are also characteristic of *Ceratopetalum* and *Schizomeria* (Cunoniaceae) (R. Barnes pers. comm.). Species of *Schizomeria* also possess secondary veins that diverge from the midvein at an approximate right angle and weakly percurrent tertiary veins demonstrating a similar angular relationship to the midvein.

Czajkowski and Rösler (1986) illustrated a similar leaf form from the Tertiary King George Island flora as 'Dicotiledonea indeterminada'. This leaf is considered similar to Morphotype 39 because it possesses an acute apex, toothed margin with rounded sinuses, semicraspedodromous venation, sinuous secondary veins diverging from the midvein at a wide acute to approximate right angle, and weakly percurrent tertiary veins. However, this leaf form has subsequently been included in *Monimiophyllum antarcticum* by Birkenmajer and Zastawniak (1989a). *M. antarcticum*, also described from the Tertiary of King George Island, does not compare well with Morphotype 39 because the tertiary veins are random reticulate, the secondary vein divergence is more acute and the teeth are monimioid in *M. antarcticum*.

Leaves illustrated as *Caldcluvia mirabilis* (Cunoniaceae) by Dusén (1908) and Czajkowski and Rösler (1986) from the Tertiary of Seymour Island and King George Island, respectively, are toothed with semicraspedodromous venation. These leaves are different to Morphotype 39 because the secondary vein divergence is moderate acute and the tertiary venation is random reticulate in *C. mirabilis*. As discussed for Morphotype 4, these Tertiary records are now considered to show greater affinities to the Proteaceae (Li 1994).

5.2.41 Morphotype 40
Figure 5.23d.
Specimen numbers
Santa Marta Formation: Fragmentary leaf: DJ147.45a (fairly good).

Description
Lamina length 27.3mm min. Lamina width 29mm min. Specimen is too fragmentary for lamina form to be assessed. Estimated leaf area 528mm^2 min., microphyllous. Apex is not preserved. Basal angle appears to be approximately 129°. On the basal right hand side of DJ147.45a (Figure 5.23d) there is a small projection with concave margins, so the leaf base is described as lobate, but the leaf base is incomplete so this determination cannot be certain. Petiole absent or not preserved. Margin appears to be crenate, indented 0.4-1mm, average 0.7mm,

approximately 8% of the distance to the midvein. Sinuses are rounded and spacing is approximately 6.5mm.

The specimen is too fragmentary for the venation type to be described. At the estimated leaf midpoint, the primary vein width is approximately 0.9mm. The size is 5% and is massive. Primary vein course appears to be straight but this is a very fragmentary specimen. There are only two alternate pairs of secondary veins preserved. The divergence angle can only be measured for the basal secondaries, which are moderate acute (46°). The variation in divergence angle along the length of the lamina and divergence angle symmetry cannot be described for this fragmentary specimen. The secondary veins appear to be of moderate thickness. The course of the secondaries appears straight and unbranched, but only a small part of the veins is preserved. The tertiary vein combination is RR. There are tertiary veins which originate on the admedial side of the secondary veins and curve to join the midvein at an approximate right angle, with an average which is unequal to the average angle of tertiary divergence from the exmedial side of the secondary veins. The tertiary venation pattern appears to be orthogonal reticulate to percurrent.

Differential characters / Discussion

This fragmentary leaf is distinguished from all others within these floras by the presence of a lobate base (basal right hand side of DJ147.45a Figure 5.23d), but it is too poorly preserved for its botanical affinities to be assessed.
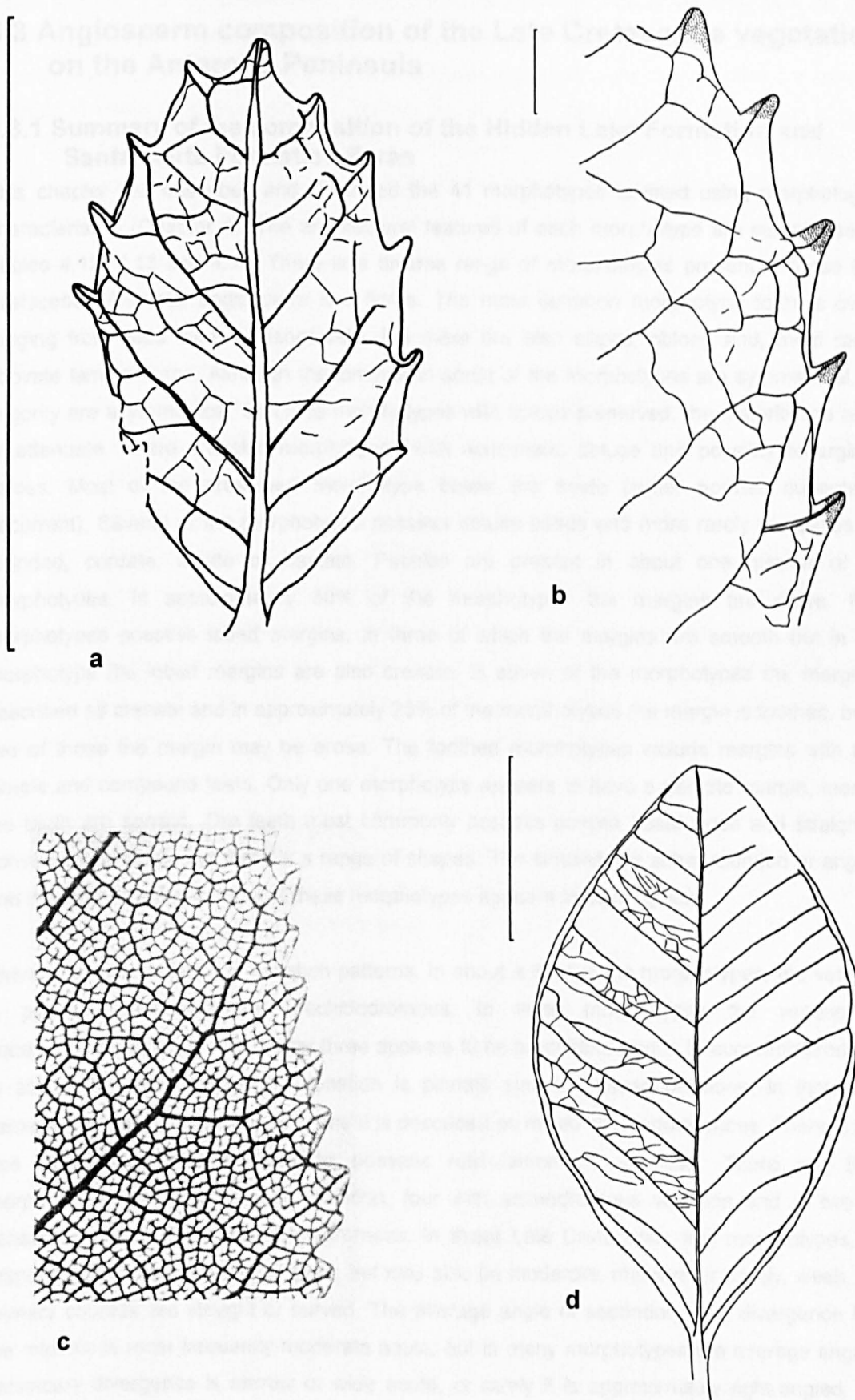
Figure 5.24 **(a)** *Ackama rosafolia* (Cunoniaceae). New Zealand. Scale bar 10mm.
(b) *Ackama rosafolia* (Cunoniaceae). New Zealand. Scale bar 1mm.
(c) *Nothofagus nitida*. x8. South America. (From Tanai 1986).
(d) *Metrosideros robusta*. (Myrtaceae). Scale bar 10mm.

5.3 Angiosperm composition of the Late Cretaceous vegetation on the Antarctic Peninsula

5.3.1 Summary of the composition of the Hidden Lake Formation and Santa Marta Formation floras

This chapter has described and illustrated the 41 morphotypes isolated using morphological characteristics (Chapter 4). The architectural features of each morphotype are summarised in Tables 4.12, 4.13 and 4.14. There is a diverse range of morphologies present in these Late Cretaceous Antarctic angiosperm leaf floras. The most common morphotype form is ovate, ranging from wide ovate to lanceolate, but there are also elliptic, oblong and, most rarely, obovate lamina forms. Although the laminae in some of the morphotypes are symmetrical, the majority are asymmetrical. Of those morphotypes with apices preserved, the majority are acute or attenuate. There are also morphotypes with acuminate, obtuse and possibly emarginate apices. Most of the preserved morphotype bases are acute (either normal, cuneate or decurrent). Several of the morphotypes possess obtuse bases and more rarely the bases are rounded, cordate, lobate or hastate. Petioles are present in about one quarter of the morphotypes. In approximately 50% of the morphotypes the margins are entire. Four morphotypes possess lobed margins, in three of which the margins are smooth but in one morphotype the lobed margins are also crenate. In seven of the morphotypes the margin is described as crenate and in approximately 25% of the morphotypes the margin is toothed, but in two of these the margin may be erose. The toothed morphotypes include margins with both simple and compound teeth. Only one morphotype appears to have a dentate margin, most of the teeth are serrate. The teeth most commonly possess convex basal sides and straight or convex apical sides, but there is a range of shapes. The sinuses are either rounded or angular and the tooth spacing in most of these morphotypes appears to be irregular.

There is a wide variation in venation patterns. In about a third of the morphotypes, the venation is pinnate camptodromous brochidodromous. In three morphotypes the venation is eucamptodromous and in a further three appears to be brochidodromous to eucamptodromous. In six of the morphotypes the venation is pinnate simple craspedodromous, in three it is semicraspedodromous and in only one it is described as mixed craspedodromous. There is also one morphotype that appears to possess reticulodromous venation. There are three morphotypes with acrodromous venation, four with actinodromous venation and in two the venation appears to be palinactinodromous. In these Late Cretaceous leaf morphotypes, the primary vein is most commonly stout, but may also be moderate, massive or, rarely, weak. The primary courses are straight or curved. The average angle of secondary vein divergence from the midvein is most frequently moderate acute, but in many morphotypes the average angle of secondary divergence is narrow or wide acute, or rarely it is approximately right-angled. The divergence of the basal secondary veins ranges from narrow acute to approximately right-angled, but is most commonly narrow acute. In most of the morphotypes the secondary vein divergence appears to vary irregularly over the length of the lamina, but in many the lowest pair of secondaries is more acute than those above and in some the secondary vein divergence is

nearly uniform. The secondary vein divergence is either symmetrical or asymmetrical. In about 20% of the morphotypes the secondary veins appear relatively fine and in about 10% they appear relatively thick. In most of the morphotypes the secondary vein courses are abruptly curved, in some they are uniformly curved and in a few they are straight. There are also secondary veins within these morphotypes that appear to be recurved or sinuous. Where the secondary veins form loops, they predominantly join the superadjacent secondary at an obtuse or approximate right angle. Outer secondary veins are present in six morphotypes. Intersecondary veins (predominantly simple) are observed in almost two thirds of the morphotypes. An intramarginal vein is clear in only one morphotype. In about half of the morphotypes the tertiary vein combination is AR and in about a third it is RR. In almost two thirds of the morphotypes the angle of tertiary vein origin on the midvein is approximately right-angled. The most frequently observed tertiary vein pattern is percurrent, usually weakly percurrent, but strongly percurrent in two morphotypes. Many of the morphotypes show random reticulate tertiary venation and rarely the tertiary venation appears orthogonal reticulate. Both randomly oriented and orthogonal quaternary and quinternary venation is present in these morphotypes, but randomly oriented higher order venation is most commonly recognised. The ultimate venation appears to be looped in at least a quarter of these morphotypes and in a few there appears to be a fimbrial vein. A variety of different tooth types are described and some of these are interpreted as possessing glands in the tooth apices. Based on leaf shapes and venation patterns, there is considered to be leaves representative of the first, third and fourth ranks within these Late Cretaceous angiosperm leaf morphotypes.

In this chapter, the distinguishing characteristics of each morphotype are outlined and comparisons are drawn with fossil and living angiosperm leaves. Table 5.1 is a summary of the diagnostic architectural features of each morphotype with examples of plant groups living today that show similarities to these Late Cretaceous morphotypes.

Table 5.1 Summary of distinguishing architectural features of these Late Cretaceous Antarctic angiosperm leaf morphotypes and examples of modern plant groups showing these characteristics.

M = Morphotype, HLF = Hidden Lake Formation, SMF = Santa Marta Formation. Percentages refer to relative abundance of each morphotype within each flora.

M	Differential architectural features	Key diagnostic characters indicative of affinity	Examples of plant groups showing these features	HLF %	SMF %
1	pinnate camptodromous brochidodromous to eucamptodromous venation; entire margin; petiolate base; oblong, elliptic or ovate form; moderate acute divergence of basal secondary veins	brochidodromous venation; entire margin; first rank (irregular venation and decurrent leaf base)	Magnoliales (e.g. Winteraceae, Annonaceae)	14	9
2	basal marginal imperfect actinodromous venation; crenate margin; cordate or obtuse cuneate base; attenuate apex; wide acute secondary vein divergence	actinodromous venation; concentrically oriented weakly percurrent tertiaries; non-glandular projections; not lobed	Sterculiaceae (Malvales)	9	5
3	pinnate camptodromous brochidodromous to eucamptodromous venation; entire margin; acute decurrent petiolate base; obovate form; massive primary vein; moderate acute secondary vein divergence; narrow acute basal secondary vein divergence; acute angle of origin of tertiary veins on midvein	brochidodromous venation; entire margin	Magnoliidae, Hamamelidae, Caryophyllidae, Dilleniidae, Rosidae	11	3
		acute decurrent base; irregularly brochidodromous venation in ascending arches; acute decurrent basal secondary veins; weakly percurrent tertiary veins	Santalales		
4	pinnate semicraspedodromous venation; toothed margin; attenuate apex; moderate acute secondary vein divergence	cunonioid teeth; semicraspedodromous venation; percurrent tertiary veins	Cunoniaceae (Saxifragales)	3	8
5	pinnate camptodromous venation; entire margin; attenuate apex; cuneate base; irregular variation in secondary vein divergence; loop-forming branches joining superadjacent secondary at an approximate right angle	brochidodromous venation; entire margin; random reticulate tertiary veins	Magnoliidae, Hamamelidae, Caryophyllidae, Dilleniidae	2	5
5B	pinnate camptodromous eucamptodromous venation; entire margin; stout primary vein; approximately right-angled origin of tertiary veins on admedial side of secondaries and on midvein	eucamptodromous venation; entire margin; ovate form; long acuminate apex; acute cuneate base; 5-8 alternate pairs of secondary veins diverging from midvein at narrow acute angle; narrow acute basal secondary veins; tertiary vein combination RR; tertiaries percurrent, closely spaced and showing an oblique relationship to midvein, angle decreasing apically; higher order venation distinct; quaternaries and quinternaries randomly oriented; marginal ultimate venation looped	Lauraceae (Laurales)	2	2
6	pinnate simple craspedodromous venation; petiolate base; massive primary vein; narrow acute secondary vein divergence; tertiary vein combination RA	simple craspedodromous venation; toothed margin	Hamamelidae, Dilleniidae, Rosidae	5	6
7	pinnate simple craspedodromous venation; emarginate apex; outer secondary veins; intersecondary veins	simple craspedodromous venation; toothed margin; regularly spaced and roughly parallel secondary veins; percurrent tertiary veins; fourth rank (regular tertiary venation); ovate form; compound serrations; many (slightly curved) outer secondary veins; higher order serrations with finer branches ending in serrations of a size which correlates to size of respective vein	Nothofagaceae (Fagales)	2	8

M	Differential architectural features	Key diagnostic characters indicative of affinity	Examples of plant groups showing these features	HLF %	SMF %
8	suprabasal acrodromous venation; toothed margin; moderate primary vein; acute angle of origin of tertiary veins on midvein	acrodromous venation; toothed margin	Laurales (Amborellaceae, Hernandiaceae, Lauraceae), Urticales (Urticaceae, Ulmaceae)	6	5
		acrodromous veins diverging at narrow acute angle to midvein; straight midvein; tertiary vein combination AR; weakly percurrent tertiaries showing an approximately right-angled relationship to midvein; looping tertiaries on exmedial side of acrodromous veins, a branch from outside of tertiary loops entering teeth; orthogonal quaternary venation	Ulmaceae (Urticales)		
9	basal acrodromous venation; entire margin; rounded petiolate base; stout midvein; acrodromous veins diverging from midvein at wide acute angle; approximately right-angled origin of tertiary veins on exmedial side of acrodromous secondary veins	single pair of basal perfect acrodromous secondary veins; entire margin; rounded petiolate base; weakly percurrent tertiary veins showing an approximately right-angled relationship to midvein; looping tertiaries on exmedial side of acrodromous veins; orthogonal quaternary veins	Lauraceae (Laurales)	2	0
10	pinnate camptodromous brochidodromous venation; entire margin; attenuate apex; acute normal to decurrent base; loop-forming branches join superadjacent secondary at an obtuse angle	brochidodromous venation; entire margin; random reticulate tertiary veins	Magnoliidae, Hamamelidae, Caryophyllidae, Dilleniidae	5	5
11	perfect acrodromous venation; entire margin; narrow elliptic to lanceolate form; acute base; massive primary vein; numerous secondary veins	acrodromous venation; entire margin; percurrent tertiary veins	Laurales (e.g. Lauraceae, Monimiaceae)	5	3
12	pinnate simple craspedodromous venation; elliptic form; acute normal base; acute angle of origin of tertiary veins on midvein; compound teeth; primary teeth served by secondary veins following a central and direct course, with accessory veins terminating at tooth apices; tertiary teeth following a deflected course serving secondary teeth	simple craspedodromous venation; regularly spaced secondaries; outer secondary veins; percurrent tertiary veins; urticoid teeth; teeth compound; elliptic form	Nothofagaceae (Fagales)	5	3
13	pinnate camptodromous brochidodromous venation; lobed margin; attenuate apex; massive primary vein	brochidodromous venation; smooth lobed margin; random reticulate tertiary veins	Caryophyllidae	2	5
14	basal marginal perfect actinodromous venation; smooth lobed margin; obtuse normal base; narrow acute basal secondary veins	actinodromous venation; entire margin; palmately lobed	Dilleniidae, Rosidae, Magnoliidae	5	1
15	pinnate mixed craspedodromous venation	-	-	2	0
16	pinnate camptodromous eucamptodromous venation; moderate primary vein; acute angle of origin of tertiary veins on admedial side of secondaries; obtuse angle of origin of tertiary veins on midvein	eucamptodromous venation; entire margin; percurrent tertiary veins	Magnoliidae, Dilleniidae, Rosidae	0	1
17	? actinodromous venation; acute angle of tertiary vein origin on midvein; arching secondary veins	arching secondary veins	Magnoliidae (e.g. Annonaceae)	2	0
18	pinnate camptodromous brochidodromous venation; entire margin; massive primary vein; moderate acute secondary vein divergence; basal secondary veins narrow acute; oblong form; acute cuneate base; right-angled origin of tertiary veins on exmedial side of secondary veins and on midvein	brochidodromous venation; entire margin; random reticulate tertiary veins; basal secondary veins more acute than those above	Laurales	2	3

M	Differential architectural features	Key diagnostic characters indicative of affinity	Examples of plant groups showing these features	HLF %	SMF %
19	pinnate camptodromous brochidodromous venation; non-entire margin; obtuse apex; elliptic form	brochidodromous venation; percurrent tertiary veins; non-entire margin; ?enrolled margin	Dilleniidae (e.g. Ericales)	0	3
20	pinnate semicraspedodromous venation; crenate margin; wide acute secondary vein divergence; outer secondary veins	semicraspedodromous venation; non-entire margin; rounded glandular teeth served by secondary vein branches showing a central and direct course, accessory veins looped; random reticulate to weakly percurrent tertiaries; oblong to elliptic form; wide acute secondary vein divergence; loop-forming branches joining superadjacent secondary at an acute angle	Elaeocarpaceae (Malvales)	3	1
21	pinnate camptodromous brochidodromous venation; entire margin; moderate primary vein; secondary vein divergence narrow acute	brochidodromous venation; entire margin; random reticulate tertiaries	Magnoliidae, Hamamelidae, Caryophyllidae, Dilleniidae	3	1
22	pinnate camptodromous brochidodromous venation; regularly spaced secondary veins; intramarginal vein; obtuse angle of origin of tertiary veins on midvein	brochidodromous venation; entire margin; intramarginal vein; acute apex; numerous subopposite to alternate pairs of secondary veins diverging from straight midvein at a moderate acute angle	Myrtaceae (Myrtales)	0	1
23	pinnate simple craspedodromous venation; simple teeth; moderate primary vein; tertiary vein combination AR; obtuse angle of origin of tertiary veins on midvein	simple craspedodromous venation; regularly spaced secondary veins; outer secondary veins; percurrent tertiary veins; non-glandular teeth; ovate form	Nothofagaceae (Fagales)	2	2
24	pinnate camptodromous brochidodromous venation; recurved or sinuous secondary veins provided with outer secondaries forming loops	brochidodromous venation; first rank (irregular venation, poor differentiation of tertiary and higher vein orders, secondary veins decurrent upon midvein, acute decurrent base, poor demarcation of petiole from blade)	Magnoliidae (e.g. Saururaceae, Aristolochiales, Ranunculales)	0	3
25	pinnate simple craspedodromous venation; right-angled origin of tertiary veins on admedial and exmedial sides of secondary veins; stout midvein; moderate acute basal secondary vein divergence; glands in tooth apices; lacking outer secondary veins; intersecondary veins	simple craspedodromous venation; percurrent tertiaries; glandular teeth	Hamamelidae, Dilleniidae, Rosidae	3	0
26	pinnate camptodromous brochidodromous to eucamptodromous venation; narrow acute basal secondary veins; secondaries recurved in parts	brochidodromous to eucamptodromous venation; entire margin	Magnoliales, Dilleniidae, Rosidae	0	2
27	pinnate simple craspedodromous venation; petiolate base; massive primary vein; narrow acute secondary vein divergence; tertiary vein combination AR		-	0	2
28	pinnate camptodromous brochidodromous venation; entire margin; secondary veins sinuous to curved; acute angle of origin of tertiary veins on admedial side of secondaries	brochidodromous venation; entire margin; random reticulate tertiary veins; basal secondaries more acute than those above; intersecondary veins	Laurales	2	1
29	pinnate camptodromous reticulodromous venation	reticulodromous venation; entire margin; random tertiary veins with tendency towards orientation parallel to secondary veins	Ebenales, Ericales	0	2
30	pinnate camptodromous brochidodromous venation; entire margin; right-angled secondary vein divergence; normal acute base; moderate primary vein; right-angled origin of tertiary veins on exmedial side of secondaries	brochidodromous venation; entire margin; reticulate tertiaries	Magnoliidae, Dilleniidae	0	2

M	Differential architectural features	Key diagnostic characters indicative of affinity	Examples of plant groups showing these features	HLF %	SMF %
31	palinactinodromous venation; straight weak midvein; obtuse cuneate petiolate base	palinactinodromous venation; margin not lobed; percurrent tertiaries; nondecurrent junction of lateral and medial primaries	Hamamelidae	2	1
32	palinactinodromous venation; lobed margin; obtuse normal base; moderate curved midvein	palinactinodromous venation; smooth lobed margin; three primary veins diverging from leaf base with two veins branching from lateral primaries; lateral primaries recurved; relatively thin secondaries and tertiaries; weakly developed ?eucamptodromous secondary veins; percurrent tertiaries; ?fimbrial vein	Laurales	2	0
33	pinnate camptodromous brochidodromous venation; entire margin; oblong form; acute apex; stout primary vein; curved secondary veins diverging from midvein at approximate right angle; acute angle of origin of tertiary veins on exmedial side of secondary veins	brochidodromous venation; entire margin	Magnoliidae, Hamamelidae, Caryophyllidae, Dilleniidae, Rosidae	0	2
34	pinnate camptodromous brochidodromous venation; symmetrical lamina; rounded base	brochidodromous venation; entire margin; ovate form; rounded base; secondary vein divergence wide acute to approximately right-angled; loop forming branches joining superadjacent secondary at obtuse angle, enclosed by tertiary and quaternary arches	Magnoliidae (e.g. Annonaceae, Monimiaceae)	2	0
35	pinnate camptodromous eucamptodromous venation; non-entire margin; moderate acute divergence of recurved secondary veins; basal pair of secondaries more acute than all those above	eucamptodromous venation; toothed margin	Dilleniidae	2	0
36	pinnate camptodromous brochidodromous venation; toothed margin; obtuse angle of tertiary vein origin on exmedial side of secondary veins	brochidodromous venation; toothed margin; elliptic to narrow obovate form; acute cuneate base; moderate acute secondary vein divergence; basal secondaries decurrent and more acute than those above; teeth glandular, acute and acuminate-convex (?monimioid)	Atherospermataceae (Laurales)	2	0
37	basal marginal actinodromous venation; non-entire lobed margin; hastate base	basal marginal actinodromous venation; weakly percurrent tertiaries concentrically oriented with respect to top of petiole; non-entire lobed margin; tertiary veins forming loops in lobe apices; ovate form; hastate base	Sterculiaceae (Malvales)	0	1
38	pinnate camptodromous brochidodromous venation; crenate margin	-	-	2	0
39	pinnate semicraspedodromous venation; non-entire margin; approximately right-angled divergence of sinuous secondary veins forming 'square' loops	semicraspedodromous venation; cunonioid teeth; percurrent tertiaries	Cunoniaceae (Saxifragales)	2	0
40	lobate base	-	-	0	1

A large component of the floras, eleven morphotypes in total, represent angiosperm leaves for which it was not possible to make any suggestions on possible botanical affinities because they possess features common to widely disparate angiosperm plant groups. Many of these Late Cretaceous leaf forms were well preserved, but leaves showing similar architecture previously published from the Antarctic Peninsula, which are generally less well preserved, have often been referred simply to *Dicotylophyllum*. A further four morphotypes within the Hidden Lake Formation and Santa Marta Formation floras show distinctive features which differentiate them from other morphotypes within the collections but are too fragmentary for detailed comparison with other fossil or living angiosperm leaves. However, there are several leaf forms that do show similarities to particular angiosperm subclasses, orders or even families.

Many of the morphotypes are common to both the Hidden Lake Formation and Santa Marta Formation floras. The dominant leaf form in both floras is considered to show similarity to the Magnoliales. Both floras also share a strong component of sterculiaceous- and lauralean-like leaf fossils. Within the Hidden Lake Formation flora, there are six different morphotypes believed to share diagnostic characters with the Laurales, four of which also occur in the Santa Marta Formation flora. However, each of the lauralean-like leaf forms possesses distinctive features, with varying shapes, venation patterns and margin styles. Two of these forms show particular similarities to leaves of the Lauraceae. There are two morphotypes within the Santa Marta Formation flora which are considered to show similarities to the Sterculiaceae, but even though one of these is represented by only a single fragmentary leaf, it is clearly very different to the other sterculiaceous type leaves, with a different shape and marginal features. Other morphotypes common to both floras include leaves showing some similarity to the Elaeocarpaceae and the Ulmaceae. The fossils studied here suggest the presence of leaves similar to the Atherospermataceae and Annonaceae, along with a Dilleniid leaf form, within the Hidden Lake Formation, but these are rare occurrences and are not found within the Santa Marta Formation flora.

There are two morphotypes with architectural characteristics typical of the Cunoniaceae. One of these is a single specimen within the Hidden Lake Formation flora that possesses clear venation patterns and marginal features but is only a fragment from the apical part of a leaf. It is possible that if this leaf had been more completely preserved it could have been grouped with the other cunoniaceous type leaves. Cunoniaceous-like leaf fossils appear to increase in number in the Santa Marta Formation. There are leaves within the Hidden Lake Formation flora with which tentative comparisons to the Nothofagaceae were made, but nothofagaceous fossils become more abundant within the Santa Marta Formation flora. There are also several morphotypes observed within the Santa Marta Formation flora which do not occur within the earlier Hidden Lake Formation flora. A leaf form showing similarities to the Myrtaceae is only present within the Santa Marta Formation flora. There are also possible Magnoliid leaves and leaf forms similar to Dilleniid orders such as the Ebenales and Ericales which are present within the Santa Marta Formation flora but not the Hidden Lake Formation flora.

Of the leaf forms sharing characteristics with modern angiosperm orders, the Magnoliales, Laurales and Malvales are dominant within the Hidden Lake Formation flora. This Coniacian assemblage shows lesser proportions of leaves similar to the Fagales, Urticales and Rosales. Within the Santa Marta Formation flora, on the other hand, leaves showing similarities to the Fagales along with the Magnoliales and Rosales are the most common. The Santa Marta Formation flora shows a much reduced lauralean-like component in comparison to the Hidden Lake Formation flora. There are also slightly lower proportions of leaves similar to the Malvales and Urticales in the Santa Marta Formation flora and this Santonian assemblage includes a morphotype with architecture suggestive of affinity with the Myrtales, of which there is no evidence in the earlier flora. In numbers of taxa, the Magnoliidae are clearly dominant in the Hidden Lake Formation, with fewer Hamamelidae, Dilleniidae, and Rosidae. In the Santa Marta Formation flora, there are more even proportions of Magnoliidae, Hamamelidae and Dilleniidae, with a small number of Rosid taxa.

6 Palaeoclimatic interpretation of the leaf floras

6.1 Introduction

This chapter presents the results of several different approaches to determine palaeoclimatic conditions on the Antarctic Peninsula during the Late Cretaceous.

These fossil plants from the Cretaceous of Antarctica are important in studies of global climate change. Polar climates have a profound effect on global atmospheric and oceanic conditions. The polar regions are especially interesting because these are the areas most sensitive to climate perturbations. Equatorial temperatures have remained relatively constant over earth history while the polar climates have ranged from intense phases of glaciation to times of warmth and the absence of major ice caps (Francis and Frakes 1993). The polar regions are the first affected by subtle changes in global climate and so this is where evidence of small-scale climate variability may be most clearly recorded (Francis 1999).

During the Cretaceous the Earth was in a major greenhouse state and some of the warmest episodes ever known were experienced, characterised by a lack of significant ice in high latitudes, warm oceans and the presence of warmth-adapted vegetation in the polar regions (Francis and Frakes 1993). Forests thrived near the poles despite the seasonal stress of polar light cycles (Askin and Spicer 1992, Francis 1999). However, the Cretaceous was not unvaryingly warm and equable, with a cooler period in the Early Cretaceous and substantial cooling in the Maastrichtian (Crame 1994). Francis and Frakes (1993) reviewed conflicting evidence of global trends and timing of peak temperatures during the warmer Late Cretaceous. The floras studied here from the Coniacian to Santonian of the Antarctic Peninsula provide new information on periods of warmth in the high southern latitudes.

Plants interact with and have profound effects on the Earth's atmosphere and hydrological cycle. Individual plant species and plant communities are morphologically and physiologically adapted to their environment, most strongly to climate, and plant fossils, therefore, are an excellent record of past climates (Askin 1992). Many living organisms have restricted tolerances to temperature and rainfall amounts, but plants are the most sensitive indicators of terrestrial climate conditions because they are not mobile and so they have to be well adapted to local conditions to survive. If not, they are either killed directly, e.g. by desiccation, or are outcompeted by better adapted plants.

Evidence of palaeotemperature from fossil plants is especially useful because it provides an independent estimate of climate on land. The data from this study supplements the ocean palaeotemperature curve for the Antarctic Peninsula known from oxygen isotope records (Ditchfield *et al.* 1994). Marine palaeotemperature records preserve a more global signature, whereas plant fossils provide more detail (Francis 1999). The only other published data for terrestrial climates of the Cretaceous Antarctic Peninsula are based on geochemical analyses of

clay minerals (Dingle and Lavelle 1998), but these require knowledge of the palaeoclimate from palaeofloras before they can be applied. Dingle and Lavelle (1998) considered that since published palaeobotanical data for the Late Cretaceous to Eocene of the Antarctic Peninsula were indicative of humid to very humid conditions, fluctuations in degrees of chemical weathering could be interpreted as a signal of ambient temperatures.

Angiosperm leaf floras can be used to determine qualitative and quantitative assessments of the ancient climates under which the plants grew. There are a variety of approaches (Wolfe 1979, 1993, Upchurch and Wolfe 1987b, Wolfe and Upchurch 1987, Spicer 1990a,b, Wing and Greenwood 1993, Wiemann *et al.* 1998):-

- Nearest Living Relative (NLR)
- Leaf margin analysis (Simple Linear Regression, SLR)
- Leaf apex style studies ('drip tips')
- Leaf size (and Leaf Size Indices, LSI, and SLR)
- Multivariate analyses (Climate-Leaf Analysis Multivariate Program, CLAMP, and Multiple Linear Regression, MLR)

Palaeoclimate estimates for the Antarctic Peninsula based on fossil angiosperm leaves have been put forward by Birkenmajer and Zastawniak (1989a,b), Rees and Smellie (1989), and Zastawniak (1994). Other plant parts used in the study of Antarctic palaeoclimates include fossil wood growth ring analyses (Francis 1986, 1991, 1996), estimates based on palynological data (Askin 1989a, Dettmann 1989, Askin and Spicer 1992, Cao 1992), and plant cuticle evidence (Askin 1992). Francis and Poole are also currently investigating the potential of angiosperm wood anatomy in palaeoclimatic studies of the Cretaceous and Tertiary of the Antarctic Peninsula.

In this chapter the Late Cretaceous Antarctic angiosperm leaves are analysed using NLR, SLR leaf margin and leaf size analyses and MLR methods.

6.2 Nearest Living Relative methods

The Nearest Living Relative (NLR) approach involves assigning a fossil plant organ to a modern group and simply extrapolating back the climatic tolerances and habitat preferences of the extant taxa (Spicer 1990a, Chaloner and McElwain 1997). Qualitative, and in some cases quantitative, assessments of palaeoclimates can be derived (Askin 1992), but there are problems with this approach:

- The NLR approach should be applied to genera, or rather species, because tolerances of higher plant groups are considered too broad (Spicer 1990a). However, in this study of Late Cretaceous angiosperms, the fossil leaves are referred only to morphotypes. Leaf architectural characteristics indicating similarity with modern subclasses, orders and families are outlined in Chapter 5, but confirmation of possible botanical affinities is required.

- The analogy to modern plants assumes evolutionary stasis but ecological preferences may have changed through time or there may be other factors, such as human disturbance, influencing the distribution of modern plants. Today angiosperms are dominant in most areas of the world, but during the Cretaceous they were rapidly diversifying within vegetation dominated by gymnosperms and ferns. As an example, the Olacaceae are now restricted to tropical Africa, Asia and America, but during the Maastrichtian the pollen of this family, *Anacolosidites,* was widespread from low to high latitudes in the northern and southern hemispheres (Askin 1989a).

- Much less is known about the climatic tolerances of Southern Hemisphere floras than those in the Northern Hemisphere and there is no analogous vegetation growing at these high southern latitudes today (Francis 1999).

Despite these difficulties, the NLR method may provide some useful information when no other evidence is available or may complement data from other sources.

Results

In Chapter 5, comparisons were drawn between the Late Cretaceous Antarctic morphotypes and the leaves of living angiosperms. Although the fossils cannot confidently be assigned to modern families or orders, the climates inhabited today by examples of plant groups with which the morphotypes share architectural characteristics are provided for comparison with the results from palaeoclimate interpretations based on leaf physiognomy. Most are Southern Hemisphere types that can be found in warm temperate and subtropical zones. Reference sources consulted for modern plant distribution include Cronquist (1981), Heywood (1985) and Mabberley (1990).

- The majority of species of the Magnoliales are trees, shrubs or woody vines inhabiting tropical or warm temperate moist and equable climates. The Winteraceae are, however, characteristic of wet tropical montane to cool temperate rain forests bordering the South Pacific, e.g. Tasmania and New Zealand.

- Sterculiaceae is a tropical to subtropical family of trees and shrubs, rarely herbs or lianes, extending throughout Australia, south Asia, Africa and northern South and Central America. Webb (1959) noted that trees of the Sterculiaceae growing in Australia require moderate moisture.

- The Laurales are trees, shrubs and woody vines with the vast majority of species occurring in tropical or warm temperate regions with a moist equable climate. Members of the Lauraceae are widespread in lowland to montane rain forests of tropical and subtropical regions, in particular southeast Asia and Brazil. Some genera do, however, occur in temperate regions.

- The Elaeocarpaceae is a widespread family of tropical and subtropical trees and shrubs present in eastern Asia, Indomalaysia, Australasia, the Pacific area, South America and the West Indies, but missing from Africa.

- Trees and shrubs of the Ulmaceae are a north temperate, subtropical or tropical family. However, the distribution of the Ulmaceae has been separated into two groups and the

genus considered similar to the Late Cretaceous fossils (*Celtis*) belongs to the group that is not characteristic of Northern Hemisphere temperate regions.

- Genera of the Atherospermataceae today inhabit tropical to temperate regions of South America and Australia.

- The Annonaceae is a large family of mainly tropical trees and shrubs especially characteristic of lowland evergreen forests of the Americas, Africa, south Asia and Australasia.

- The Cunoniaceae are today native to the Southern Hemisphere, mainly occurring as trees, shrubs or woody climbers in tropical and warm temperate Australia, New Guinea and New Caledonia with a few genera in South Africa and tropical South America.

- The Myrtaceae are small shrubs to large trees found in subtropical and tropical regions around the world including South America, Africa, south Asia and southern Europe. They dominate forests in eastern and southwestern Australia, where they are also well developed in temperate climates. Certain Myrtaceae are adapted to aridity, but others require moderate moisture (Webb 1959).

- The Nothofagaceae dominate in temperate forests along the southern Andes and in Tasmania. *Nothofagus* trees can today survive extreme cold, up to -22°C (Hill *et al.* 1996), and are considered to represent cooler climates (Francis 1999), although there are modern species living in tropical New Guinea and New Caledonia (Tanai 1986).

6.3 Methods using leaf physiognomy

The analysis of angiosperm leaf physiognomy (e.g. leaf margins, size and shape) is an especially useful tool in the determination of palaeoclimates because it does not require the accurate identification of fossil leaf floras (Spicer 1990a, Askin 1992). Leaf physiognomy-climate relationships are also considered more stable through geologic time (Spicer 1990b). Methods independent of taxa have been developed to provide quantitative estimates of mean annual temperature and water availability. These methods extend early observations on the correlation of leaf margin and leaf size with environment in modern vegetation by Bailey and Sinnott (1916) and Webb (1959).

6.3.1 Leaf margin analysis

Leaf margin analysis is considered one of the most useful techniques in terrestrial palaeoclimate reconstruction (Askin 1992). Early work on extant dicotyledonous angiosperm floras from all around the world by Bailey and Sinnott (1916) showed that species with entire margined leaves are dominant in warm tropical environments, while leaves with non-entire margins predominate in cooler temperate regions.

| entire | entire | non-entire | non-entire |
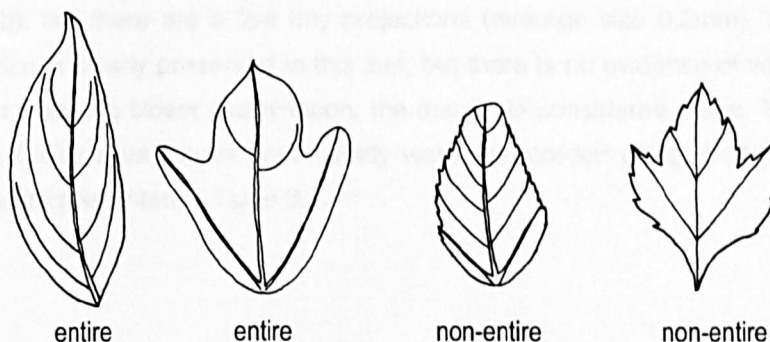
Figure 6.1 Entire margined and toothed margined leaves.

The terms 'entire' and 'non-entire' are potentially misleading in leaf margin analysis studies. The method of determination of margin style by different workers is a possible source of error in these analyses. In terms of systematic description of the nature of a leaf margin, 'entire' refers to only smooth leaf margins without noticeable projections or indentations (Hickey 1979). 'Non-entire' margins would then include all other leaf margin features such as lobes, crenations, teeth and spines. Bailey and Sinnott (1916) had originally used non-entire to refer to all leaf margin types other than smooth, i.e. lobes were regarded as non-entire. However, in modern leaf margin analysis, the relationship of non-entire margins to mean annual temperature (MAT) is based on only those non-entire leaves with toothed margins (Wolfe and Upchurch 1987). Lobed margins are only considered non-entire if the margin of the lobes is also toothed, and spines are also included in the 'entire' category (Figure 6.1).

The distinctions on marginal style in modern palaeoclimate analysis are based on presumed physiological adaptations. A triangular tooth is considered the most efficient way of allowing venation to support and supply water to the thin deciduous leaves in cool regions (Jacobs 1999 and references therein). The presence of spines, on the other hand, is considered insignificant in climate analysis, since these are believed to be primarily a defence against herbivory (Wolfe 1993). This is not an important consideration in this study of Late Cretaceous leaves because none of the morphotypes possess spines.

To avoid ambiguity in this study, the terms 'entire' or 'non-entire' are not used and instead simply presence or absence of teeth is recorded. The recognition of teeth, however, is also rather subjective. The margins of the morphotypes described in Chapter 5 were defined using Hickey's (1979) classification and, for most of the leaves observed, this does not contradict with modern methods in leaf margin analysis (Wolfe 1993). An exception is the leaf margins referred to as crenate in this study. Using Wolfe's (1993) terminology, these would be included within the toothed category as rounded teeth. Where there is doubt about the nature of the margin, confidence in the recording of teeth is increased where there is evidence of a vein terminating at the margin (Wilf 1997, E. Kennedy pers. comm.). For example, Morphotype 19 appears to possess rounded projections (Figure 5.14e,f). More detailed observation (Figure 5.14g) shows the tertiary vein terminating at the apex of a projection, and so this margin is classed as toothed. Only a rather small proportion of the margins are preserved in the single leaf of Morphotype 17

(Figure 5.14a,b), but there are a few tiny projections (average size 0.2mm), some appearing pointed. Venation is clearly preserved in this leaf, but there is no evidence of veins in these tiny projections. So following closer examination, the margin is considered entire. The leaf margins of all the Late Cretaceous leaves under study were re-recorded using Wolfe's (1993) criteria and the results are presented in Table 6.1.

Results

For the Hidden Lake Formation and the Santa Marta Formation floras, the margins of each morphotype were recorded as toothed or untoothed (Table 6.1). A total percentage for each flora was then calculated.

Morphotype	Teeth	Hidden Lake Formation	Santa Marta Formation
1	Absent	✓	✓
2	Present	✓	✓
3	Absent	✓	✓
4	Present	✓	✓
5	Absent	✓	✓
5B	Absent	✓	✓
6	Present	?	✓
7	Present	✓	✓
8	Present	✓	✓
9	Absent	✓	-
10	Absent	✓	✓
11	Absent	✓	✓
12	Present	✓	✓
13	Absent	✓	✓
14	Absent	✓	✓
15	Present	✓	-
16	Absent	-	✓
17	Absent	✓	-
18	Absent	✓	✓
19	Present	-	✓
20	Present	✓	✓
21	Absent	✓	✓
22	Absent	-	✓
23	Present	✓	✓
24	Absent	-	✓
25	Present	✓	-
26	Absent	-	✓
27	Present	-	✓
28	Absent	✓	✓
29	Absent	-	✓
30	Absent	-	✓
31	-	?	?
32	Absent	✓	-
33	Absent	-	✓
34	Absent	✓	-
35	Present	✓	-
36	Present	✓	-
37	Present	-	✓
38	Present	✓	-
39	Present	✓	-
40	-	-	?

Table 6.1 The nature of the leaf margins in the 41 morphotypes of the Hidden Lake Formation and Santa Marta Formation floras.

Morphotype 6 was not included in the analysis of the Hidden Lake Formation flora because although the leaves share features with the Santa Marta Formation specimens in which teeth are present, the Hidden Lake Formation specimens are poorly preserved and the margins are unclear. The margins of morphotypes 31 and 40 are too incompletely preserved for them to be clearly categorised in this analysis. Table 6.2 shows the proportion of each flora with untoothed or toothed margins expressed as a percentage of morphotypes and of individual leaves.

Although the number of leaves within each morphotype is variable, with relative abundances within the floras ranging from 1-14%, it is interesting that both morphotypes and individual leaves give very similar results. In the Santa Marta Formation flora, the majority of both morphotypes and individuals are untoothed. In the Hidden Lake Formation flora, the proportion of untoothed margins is the same for both morphotypes and individuals.

Flora	No teeth		Teeth	
	Morphotypes	Individuals	Morphotypes	Individuals
Hidden Lake Formation	15 (54%)	54%	13 (46%)	46%
Santa Marta Formation	18 (62%)	55%	11 (38%)	45%

Table 6.2 Proportion of morphotypes and individual leaves with and without toothed margins for the two Late Cretaceous floras studied.

Based on extensive studies of living humid to mesic eastern Asian forests, Wolfe (1971, 1979) established a linear relationship between mean annual temperature (MAT) and the proportion of entire-margined species, illustrated in Figure 6.2. This relationship only breaks down in areas of low moisture availability, in very cold or arid regions, where there is an increased proportion of entire margined species (Gregory and McIntosh 1996). The relationship established for the Northern Hemisphere is an increase of 1°C for every 3% increase in entire margined species, with 60% corresponding to a MAT of 20°C (Wolfe 1979, Wolfe and Upchurch 1987). A higher proportion of evergreen plants is thought to be reflected in higher percentages of entire margined species in the modern vegetation of the Southern Hemisphere (Wolfe 1971, 1979, Wolfe and Upchurch 1987, Spicer 1990a). Using relatively limited data, Wolfe (1979) adjusted his curve so that an increase of 4% in smooth margined species corresponds to a 1°C increase in MAT, with 68-70% entire margined species approximating a MAT of 20°C. Leaf margin analysis has been applied in many studies of palaeoclimate (e.g. Wolfe and Upchurch 1987, Rees and Smellie 1989, Spicer and Parrish 1990).
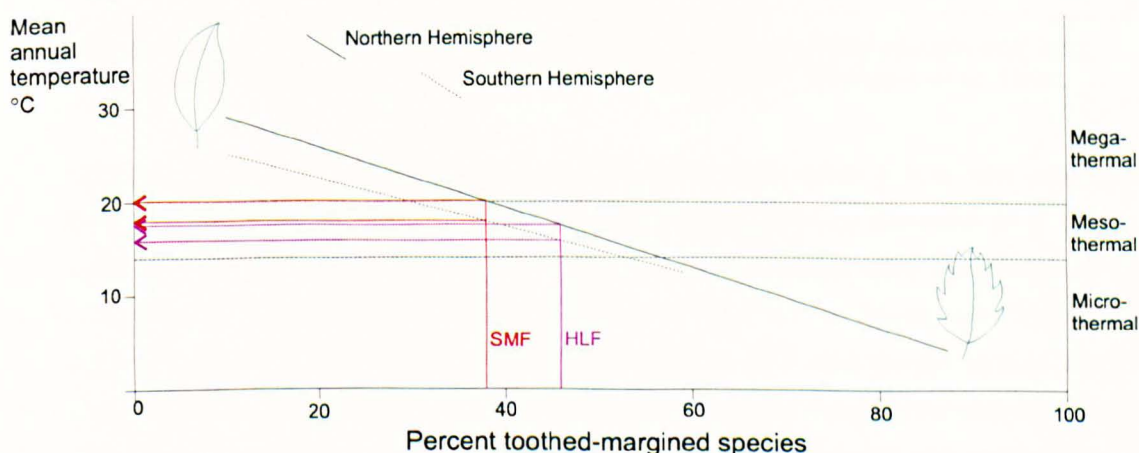
Figure 6.2 Relationships between the percentage of taxa with toothed margins and MAT for modern floras from the Northern and Southern Hemispheres. Redrawn from Spicer (1990a) with the x-axis label corrected.
HLF – Hidden Lake Formation flora, SMF – Santa Marta Formation flora.

Defining an 'adequate sample', Wolfe (1971) considered that a sample of 20 to 29 taxa, as in this study, allowed leaf margin percentages to be established with a degree of precision of ±10%. The percentage of Late Cretaceous leaves with toothed margins is plotted on the graph in Figure 6.2 and the results are presented below:

Northern Hemisphere curve:

- Hidden Lake Formation flora – MAT = 18.0 ±1.8°C.
- Santa Marta Formation flora – MAT = 20.7 ±2.1°C.

Southern Hemisphere curve:

- Hidden Lake Formation flora – MAT = 16.3 ±1.6°C.
- Santa Marta Formation flora – MAT = 18.3 ±1.8°C.

6.3.1.1 Simple linear regression models based on leaf margin analysis

The relationships demonstrated between leaf margin and MAT plot as a straight line (e.g. Figure 6.2) (Wolfe 1979), so several workers have converted this information to simple linear regression (SLR) equations. Some of these are given in Table 6.3.

SLR	Source
MAT (°C) = (0.306 x %entire) + 1.141 r^2=0.983, p<0.001, s.e. = ±0.788°C	Wing and Greenwood (1993) derived the equation from Wolfe's (1979) plots for East Asian forests.
MAT (°C) = (0.22 x %entire) + 4.4 r^2=0.75	Wiemann et al. (1998) derived the equation from Greenwood's (1992) plots for Australian floras.
MAT (°C) = (0.286 x %entire) + 2.24 r^2=0.94, p<0.0005, s.e. = ±2.0°C	Wilf (1997) for temperate and tropical floras of North and South America.
MAT (°C) = (0.291 x %entire) – 0.266 r^2=0.76, p<0.0005, s.e. = ±3.4°C	Wilf (1997) derived the equation from the CLAMP data set (Wolfe 1993).
MAT (°C) = (0.244 x %entire) + 3.25 r^2=0.84, p<0.0005, s.e. = ±2.1°C	Wilf (1997) derived the equation from the CLAMP data set (Wolfe 1993) with 32 sites with coldest winter temperatures removed.

Table 6.3 SLR equations derived from relationships between leaf margin and MAT (Greenwood 1992, Wing and Greenwood 1993, Wilf 1997, Wiemann et al. 1998).

For these equations, '%entire' refers to the percentage of taxa within a flora with untoothed margins. However, although this was the definition of '%entire' given by Wiemann et al. (1998), in Greenwood's (1992) analysis of Australian forest floors lobed leaves were excluded from the entire category and non-angiospermous leaves, such as larger conifer leaves, were included in the study. The resulting relationship demonstrated between MAT and margin style is weaker than in the original data plotted by Wolfe (1979). It is not clear how the different definitions have been applied in the development of this model, so the results are regarded with some doubt. In comparisons between actual and predicted values for living forests in Florida, Wiemann et al. (1998) found that the equation derived from Greenwood's plots gave lower estimates of MAT than the Wolfe (1979) or Wilf (1997) SLRs, but the maximum errors were smaller than observed for these two models.

Results

Data from the Hidden Lake Formation and Santa Marta Formation floras were input into the three equations above and the MAT was calculated based on the percentages of morphotypes with untoothed margins within each flora. The figures entered in the equation marked Greenwood's (1992) method (b) were adjusted to take into account Greenwood's inclusion of lobed leaves in the 'nonentire' category. However, although the temperatures predicted using Greenwood (b) are included in Table 6.4, I do not consider these to be valid data because inclusion of lobed leaves is of debatable significance.

SLR		Hidden Lake Formation flora MAT (°C)	Santa Marta Formation flora MAT (°C)
Wolfe (1979) equation (Wing and Greenwood 1993)		17.7 ±0.8	20.1 ±0.8
Greenwood (1992) equation	(a)	16.3	18.0
(Wiemann et al 1998)	(b)	13.9	16.5
Wilf (1997) equation		17.7 ±2.0	20.0 ±2.0
CLAMP equation (Wilf 1997)		15.5 ±3.4	17.8 ±3.4
CLAMP equation (cold sites excluded) (Wilf 1997)		16.4 ±2.1	18.4 ±2.1

Table 6.4 Estimates of MAT for the Hidden Lake Formation and Santa Marta Formation floras calculated using SLR equations.

6.3.2 Leaf apex type

The shapes of leaf apices, including attenuate, acute, rounded and emarginate, are considered related to climate parameters. A 'drip tip' is a highly attenuated leaf apex and these are associated with high humidity. It is believed that they enhance drainage and retard the growth of epiphytes (Wolfe and Upchurch 1987, Spicer 1990a, Wolfe 1993).

Results

For palaeoclimatic analysis the shapes of the leaf apices were re-examined and classified according to CLAMP definitions (Wolfe 1993). Unfortunately, the leaf apex is fragile and usually the most frequently missing part. The apices are present in approximately 25% of the leaves of the Late Cretaceous floras studied here. However, once the specimens were grouped into taxa (Chapter 4 and 5), it was possible to describe the apical styles of more than 50% of the morphotypes. The apical styles of 19 of the 30 Hidden Lake Formation flora morphotypes and 18 of the 31 Santa Marta Formation flora morphotypes were categorised and the results are presented in Appendix 4, Table A4-2 and summarised in Table 6.14. A high percentage of the morphotypes with apices intact possess attenuate apices:

• Hidden Lake Formation flora – 53%

• Santa Marta Formation flora – 44%

This evidence is considered to reflect persistent humidity on the Antarctic Peninsula during the Late Cretaceous.

6.3.3 Leaf Size

Angiosperm leaf size is strongly related to temperature, humidity and light levels (Spicer 1990a). Large leaves occur in warm humid understoreys and decreasing size has been correlated with lower moisture availablility, lower temperatures and increased light levels (Webb 1967, Dolph and Dilcher 1980, Spicer 1990a). Testing relationships between various leaf characters and climate parameters in modern vegetation, Wiemann *et al.* (1998) concluded that leaf size is one of the most important predictors of precipitation.

6.3.3.1 Analysis of leaf size distribution according to Webb's classification

Following the classification of modern Australian rain forests, Webb (1959) categorised vegetational types using leaf size distribution. Tropical, subtropical, and temperate rain forest formations were separated by the dominance of one of three leaf size categories. Webb (1959) simplified an earlier scheme by Raunkiaer (1934), erecting three main classes (Table 6.5):

Leaf size category	Length, l (mm)	Area, A (mm^2)
microphyll	l < 76	A < 2025
notophyll	76 ≤ l >127	2025 ≤ A >4500
mesophyll	l ≥ 127	A ≥ 4500

Table 6.5 Leaf size classes (Webb 1959).

Results

The area of all of the specimens from the Hidden Lake Formation and Santa Marta Formation floras was measured using image analysis software (ImageJ). This data is presented in Appendix 2, Table A2-3 and A2-4 and is charted using the leaf size categories defined above in Figure 6.3.
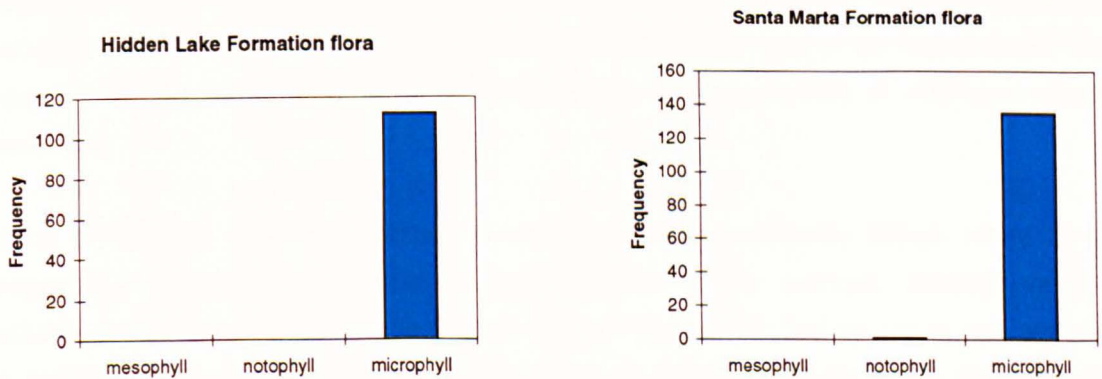
Figure 6.3 Leaf specimen sizes within the Hidden Lake Formation and Santa Marta Formation floras.

All the leaves are rather small with all of the Hidden Lake Formation specimens falling within the microphyllous category. Almost all of the Santa Marta Formation specimens are also microphyllous, with only one specimen within the notophyllous size bracket. Since there was almost no variation observed between all of the specimens, it was not necessary to display data for leaf morphotypes as well as individual leaf specimens.

This data was then compared to Webb's analysis of modern floras from Australia (Figure 6.6). Vegetation with predominantly microphyll size or smaller leaves is characteristic of cool or warm temperate rain forest. The microphyll leaf size percentages of 100% (Hidden Lake Formation) and 99% (Santa Marta Formation) correspond to the microphyll mossy thicket (MMT) and microphyll mossy forest (MMF) respectively. These subformations are characterised by simple toothed margined leaves and a sparse or absent understorey and lower tree layer with a canopy dominated by a single species, Nothofagus. These vegetation types are typical of cool temperate regions with mean annual temperatures of 10-13°C, as seen in Tasmania for example. They also occur at high altitudes in subtropical or tropical climates.

Palaeoclimatic interpretations based on leaf size within fossil assemblages are, however, strongly influenced by taphonomic biases. Within the Hidden Lake Formation and Santa Marta Formation floras, only about 25% of the specimens are almost whole leaves (Figure 2.4). The remaining specimens have suffered varying degrees of fragmentation. The area measurements given above represent a mix of whole leaves or fragments of leaves.

Antarctic dicotyledonous angiosperm leaf systematic studies frequently rely on fragmentary material because of the lack of suitable preservational facies. It was considered important to include these specimens in the study in an attempt to evaluate the taphonomic bias. There may be just one small leaf size category represented, but although all the fragments are roughly similar in size, it is believed that the original leaves would have shown a considerable size range. It seems likely then that the predominance of small leaves is biased by taphonomic processes and is not a true representation of the leaf size distribution within the parent vegetation. This suggests that these sorts of palaeoclimate estimates are rather unreliable without a consideration of taphonomy. The original leaf size of many of the leaves would have been much larger and therefore the results above are an estimate of minimum climatic conditions.

Using multivariate statistical methods it was possible to confidently assign many of the fragmentary specimens to morphotypes (see Chapter 4). For example, although venation patterns are unclear in D8754.8.58a (Figure 6.4), this fragmentary leaf specimen was assigned to Morphotype 2 using leaf architectural characters such as the shape of the leaf base, the crenate margin, the curved unbranched secondary vein reaching the margin and the angles of origin of the tertiary veins. It was then possible to reconstruct the original size and shape of the leaf fragments, as illustrated in Figure 6.4.
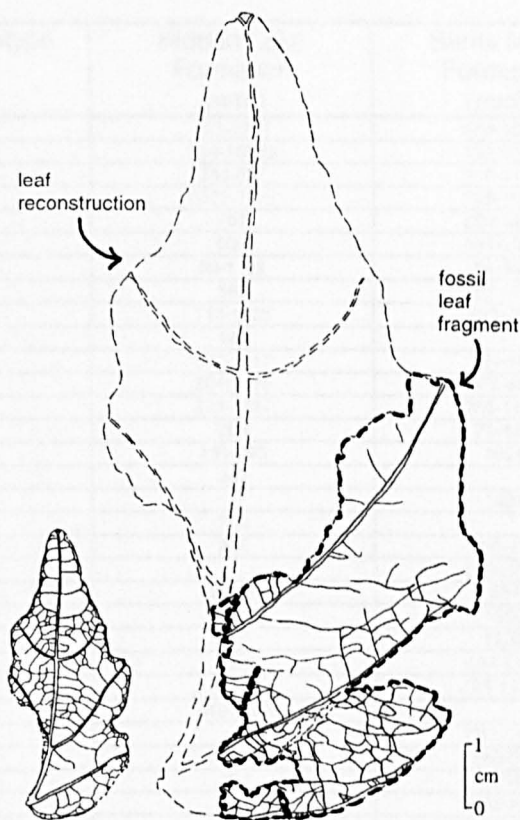
Figure 6.4 Reconstruction of a fragmentary leaf (D8754.8.58a, see Appendix Volume 2 p42, 124) within the Hidden Lake Formation flora (Morphotype 2).

It was possible to reconstruct much of the fragmentary material by filling in missing areas using the leaf margins present. For each leaf the outline drawn was always a minimum estimate. The area was then measured using image analysis software. It was generally assumed that the leaves were roughly symmetrical, unless it was obvious that this was not the case. For the more fragmentary leaves within each morphotype, the original leaf length was estimated using the average length/width ratio calculated for that morphotype based on observations of almost whole leaves. The leaf blade area was then estimated using the following equation cited by Webb (1959):   Area = 2/3 x length x width

These methods produced minimum estimates of the true original leaf size maximums. For each flora the minimum and maximum area of each morphotype was recorded. This data is presented in Table 6.6. The morphotypes of each flora were assigned to the size classes given in Table 6.5. As in the study of Wolfe and Upchurch (1987), the largest size for each morphotype is used in the analysis in an attempt to reduce taphonomic biases.

The charts in Figure 6.5 show the estimated size ranges of leaf morphotypes and individual leaves within each flora.

Morphotype	Hidden Lake Formation (mm^2)	Santa Marta Formation (mm^2)
1	435-1231	559-1557
2	528-10883	193-7189
3	208-627	310-1161
4	3523-3736	185-1962
5	767	260-1221
5B	603	445-2395
6	59-1122	54-855
7	383	551-2642
8	113-1635	483-753
9	130	-
10	852-2317	124-844
11	264-1005	375-827
12	378-4327	256-1472
13	204	70-482
14	131-793	1094
15	387	-
16	-	1521
17	799	-
18	265	429-832
19	-	569-2763
20	230-362	561
21	571	1550
22	-	1237
23	1304	184-1379
24	-	25-1139
25	346-1753	-
26	-	1791-2685
27	-	266-323
28	727	154
29	-	236-283
30	-	357-433
31	365	1108
32	972	-
33	-	395-504
34	119	-
35	912	-
36	352	-
37	-	839
38	96	-
39	137	-
40	-	528

Table 6.6 Range of estimated leaf sizes for each morphotype in the Hidden Lake Formation and Santa Marta Formation floras.

The colours indicate the size class to which each morphotype was assigned:
red – mesophyll, green – notophyll, blue – microphyll.
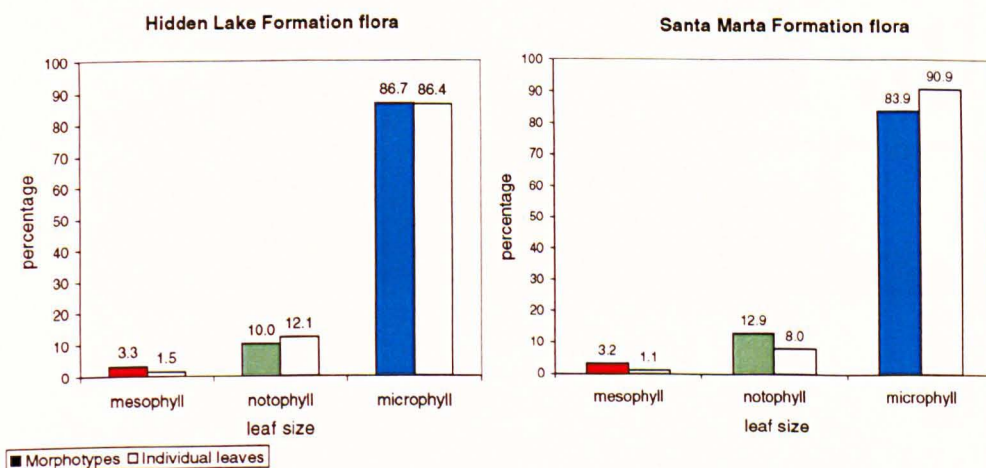
Figure 6.5 Estimated leaf sizes of morphotypes and individual leaves within the Hidden Lake Formation and the Santa Marta Formation floras.

These charts show that although all the leaf fragments are roughly similar in size, a range of original leaf sizes is represented. The results for both the Hidden Lake Formation and Santa Marta Formation floras are very similar and are therefore discussed together. Of the twelve Australian rain forest subformations defined by Webb (1959), the size distribution in the Cretaceous floras corresponds most closely with the semi-evergreen vine thicket (SEVT). The percentages of leaf characters defined for this category by Webb (1959) are given in Table 6.7. The percentage of species with notophyll and microphyll leaf sizes in the SNVF category is very different to those exhibited by the Late Cretaceous Antarctic morphotypes. However, out of all twelve subformations, the percentage of species with entire margins in the Late Cretaceous morphotypes (see Section 6.3.1) is best represented by the SNVF category.

Subformation	Mesophyll	Notophyll	Microphyll	Compound	Entire
SEVT	0-10	20-55	40-80	20-30	65-75
SNVF	0-30	55-70	0-40	10-25	40-70

Table 6.7 Leaf character distributions expressed as percentages of species for two of the twelve Australian rain forest subformations defined by Webb (1959).
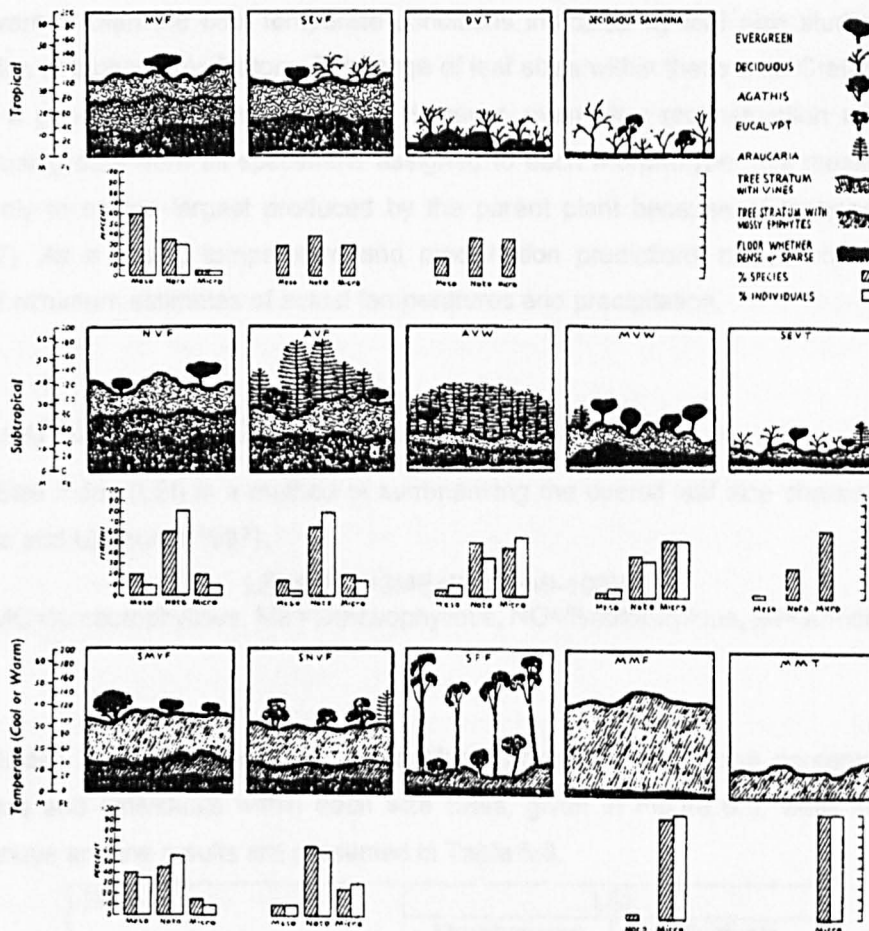
Figure 6.6 Australian rain forest subformations, showing (from left to right) increased discontinuity and simplification of tree layers away from optimal conditions. (From Webb 1959.)

The SEVT subformation is characterised by a sparse uneven canopy with occasional emergents, prominent lianes, a dense shrub understorey and a sparse ground layer. It is interesting that 'Bottle Trees' (Sterculiaceae) are common in this extant Australian subformation, since leaf forms showing similarities to the Sterculiaceae are well represented within these Late Cretaceous Antarctic floras. This vegetation type corresponds to a subtropical climate, away from optimal conditions (Figure 6.6). The SNVF subformation has trees with sparse and narrow crowns, a strong tendency to single species dominance in the upper tree layers and sclerophyllous emergents. This type of vegetation occurs in temperate or subtropical lowlands and montane tropical regions. Greenwood (1992) equated the SNVF forests to the notophyllous broad-leaved evergreen forest of Wolfe (1979), which suggests MATs of 13-20°C. The notophyllous broad-leaved evergreen forest type also shows similar foliar physiognomic characteristics and a similar floristic composition to the Late Cretaceous floras studied here, dominated by lauralean and fagalean trees.

These results demonstrate that estimates based on only the almost whole specimens gives underestimates of palaeoclimate parameters. Whole leaves are selectively preserved and are small in number. The analysis of fragmentary specimens shows that the palaeoclimate was probably warmer than the cool temperate conditions indicated by leaf size studies without a consideration of taphonomic factors. The range of leaf sizes within these Late Cretaceous floras does give a general indication of climate. However, even after reconstruction of the largest specimen using data from all specimens assigned to each morphotype, this maximum size is still not likely to be the largest produced by the parent plant because of taphonomic biases (Chapter 7). As a result, temperature and precipitation predictions based on leaf size are considered minimum estimates of actual temperatures and precipitation.

6.3.3.2 Leaf Size Index (LSI)

The Leaf Size Index (LSI) is a method of summarising the overall leaf size characteristics of a flora (Wolfe and Upchurch 1987):

$$LSI=(4MC+3ME+2NO+MI-100)/2$$
... where MC=%macrophyllous, ME=%mesophyllous, NO=%notophyllous, MI=%microphyllous

Results

For the Hidden Lake Formation and Santa Marta Formation floras, the percentages of leaf morphotypes and individuals within each size class, given in Figure 6.5, were input into the equation above and the results are presented in Table 6.8.

Flora	LSI	
	Morphotypes	Individuals
Hidden Lake Formation	8.3	7.6
Santa Marta Formation	9.7	5.2

Table 6.8 Leaf size indices (LSI) within these Late Cretaceous Antarctic Peninsula floras.

The LSI values obtained in this study of Antarctic angiosperm leaves are very low in comparison to those given for other Late Cretaceous and modern floras. These figures are much lower than the value of 75 approximated for extant megathermal vegetation experiencing abundant precipitation (Webb 1959, Wolfe and Upchurch 1987). Using various palaeobotanical methods, Wolfe and Upchurch (1987) made interpretations of palaeoclimatic conditions at various latitudes during the Late Cretaceous. Estimates of palaeotemperatures based on leaf margin analysis were made and, along with an assessment of apex forms, leaf size indices were used principally to infer relative moisture availability. Subhumid megathermal conditions were suggested for Late Cretaceous southeastern North American floras with LSI values of between 22 and 52. Of the LSI values given by Wolfe and Upchurch (1987), some of the closest to those obtained in this study of Antarctic leaves came from western Greenland. Along with results from leaf margin analysis and the greater number of leaf forms with emarginate rather than attenuate apices, the Greenland LSI values of 12-24 were considered to reflect a subhumid mesothermal environment. However, in these Late Cretaceous Antarctic floras, emarginate apices are very rare and attenuate apices are relatively common (Section 6.3.2, Appendix 4, Table A4-2), so the very low LSI is not considered to indicate very low moisture levels.

In a plot of LSI versus latitude for the Late Cretaceous constructed by Wolfe and Upchurch (1987), the lowest leaf size indices (about 20-25) occur at roughly 55-65°N, where the warm month mean drops below 20°C. Greenwood (1992) quoted LSI values for various extant forest types in Australia. The closest values (12.5-16.7) to those obtained in this Antarctic study were for simple notophyll vine forest in New South Wales at an altitude of 800m where the MAT is about 15°C. Greenwood (1992) found strong correlation between LSI and MAT in modern leaf litter from Australia. Using this relationship based on individual leaves gives estimates of MAT of approximately 12°C for the Hidden Lake Formation and 11°C for the Santa Marta Formation. However, it has been stressed by many authors (including Greenwood 1992) that mean annual temperatures obtained using LSI for individual leaves are unreliable for allocthonous assemblages. The taphonomic biases (Chapter 7) experienced by these transported fragmentary fossil assemblages mean that the leaf size indices obtained are probably much lower than the actual values for the parent vegetation. These factors alone may explain why the LSI values calculated are lower than expected for mesothermal vegetation. In this study, therefore, leaf size indices cannot be used to infer a lack of moisture and the palaeotemperatures interpreted are minimum estimates of the actual temperatures on the Antarctic Peninsula during the Late Cretaceous.

6.3.3.3 Simple linear regression models based on leaf size

Based on the CLAMP data set (Wolfe 1993), Wilf et al. (1998) derived a linear relationship between leaf size and mean annual precipitation (MAP).

$$MAP = (6.18 \times \%large\ leaves) + 47.5$$

In this equation, '%large leaves' refers to the percentage of species in an assemblage with a leaf size of mesophyll I or larger, (using the CLAMP area classification, i.e. area $\geq 3516mm^2$).

Results

Based on maximum estimated leaf area (Table 6.6), the percentages of morphotypes with large leaves within the Hidden Lake Formation and Santa Marta Formation floras were input into the equation above and the results indicating amounts of mean annual precipitation are given in Table 6.9.

Flora	Percentage of morphotypes with large leaves ($\geq$3516mm^2)	MAP (cm)
Hidden Lake Formation	10	109.3
Santa Marta Formation	3.2	67.3

Table 6.9 Percentages of morphotypes with large leaves within these Late Cretaceous Antarctic floras and estimates of mean annual precipitation calculated using the CLAMP SLR equation of Wilf et al. (1998).

However, multiple linear regression models created to predict precipitation parameters based on the CLAMP data set (e.g. Wing and Greenwood 1993) have been tested on living vegetation and have often been found to overestimate precipitation (Jacobs and Deino 1996, Wilf 1997, Wilf et al. 1998). Wilf et al. (1998) considered that an improved model might be constructed from a re-examination of the univariate relationship between leaf size and moisture availability using data from a wide variety of climates and vegetation types. Based on samples from subtropical and tropical South America, the West Indies, West Africa and North and Central America, Wilf et al. (1998) derived a simple linear regression model to predict MAP from the mean of the natural logarithms of the species' leaf area:

$$\ln(MAP) = (0.548 \times MlnA) + 0.768$$
$$r^2=0.760, p=10^{-15}, s.e. = \pm0.359cm$$

Results

The natural logarithm of the maximum estimated leaf area of each morphotype was calculated for both floras. Again the largest size for each morphotype (given in Table 6.6) was used in an attempt to minimise the effects of taphonomic biases. The mean of these values was then input into the equation above and the resulting estimates of mean annual precipitation are presented in Table 6.10.

Flora	Mean ln leaf area (mm^2)	MAP (cm)
Hidden Lake Formation	6.53	77.2 (53.9-110.5)
Santa Marta Formation	6.92	95.6 (66.8-136.9)

Table 6.10 Mean natural logarithm of leaf area for these Late Cretaceous Antarctic floras and estimates of mean annual precipitation calculated using the leaf area analysis SLR equation of Wilf et al. (1998).

MAP estimates incorporating standard errors are given in parentheses.

Based on their data set, Wilf et al. (1998) also derived the following equation using the percentage of species with large leaves in a flora to predict MAP:

$$MAP = (3.77 \times \%large\ leaves) + 47.0$$

In this equation, '%large leaves' refers to the percentage of species in an assemblage with a leaf size of mesophyll or larger, (using the Webb (1959) classification, i.e. area $\geq$4500mm^2).

Results

Based on maximum estimated leaf area (Table 6.6), the percentages of morphotypes with large leaves within the Hidden Lake Formation and Santa Marta Formation floras were input into the equation above and the results indicating amounts of mean annual precipitation are given in Table 6.11.

Flora	Percentage of morphotypes with large leaves ($\geq 4500mm^2$)	MAP (cm)
Hidden Lake Formation	3.3	59.4
Santa Marta Formation	3.2	59.1

Table 6.11 Percentages of morphotypes with large leaves within these Late Cretaceous Antarctic floras and estimates of mean annual precipitation calculated using the large leaf SLR equation of Wilf *et al.* (1998).

Since all the simple linear regression models used in this study to predict precipitation are based on leaf size, a consideration of the taphonomic biases (Chapter 7) suggests that the results given in Table 6.9, Table 6.10 and Table 6.11 are minimum estimates of actual precipitation on the Antarctic Peninsula during the Late Cretaceous.

6.3.4 Leaf lobing

Wolfe and Spicer (1999) illustrated a nonlinear relationship between leaf lobing and MAT. Lobed leaves are most common in warm microthermal vegetation (MAT 4-12°C) and become more infrequent in warmer or cooler climates.

Results

In both floras, 10% of the leaves possess lobed margins (see Table 6.14), which using Spicer's chart, offers an estimate of MAT of 15°C for both the Hidden Lake Formation and Santa Marta Formation floras. However, since the preservation of lobed leaves is strongly influenced by taphonomic biases (Chapter 7), these results are tentative.

6.3.5 Multivariate analyses

Many workers (e.g. Askin 1992, Wolfe 1993, 1995, Gregory and McIntosh 1996, Wiemann *et al.* 1998, Wolfe and Spicer 1999) consider that simultaneously analysing multiple leaf characters leads to improved palaeoclimatic interpretations.

6.3.5.1 Climate-Leaf Analysis Multivariate Program (CLAMP)

The complex relationships of climatic parameters and leaf physiognomy are considered by Wolfe (1995) and other researchers to be most accurately and precisely defined by the Climate-Leaf Analysis Multivariate Program (CLAMP) of Wolfe (1993). Originally 29 leaf characters, relating to margin, size, apex, base, and shape, were used to estimate temperature and precipitation variables. Herman and Spicer (1996, 1997) and Kovach and Spicer (1996) used the CLAMP database to predict climate variables using two additional leaf size characters. The relations of each character to environmental variables are typically nonlinear, so ordination methods such as Correspondence Analysis and Canonical Correspondence Analysis are used to represent leaf character states and accompanying meteorological data for the extant forest samples on ordination axes. The two principal axes are considered to represent temperatures and water stress (Wolfe 1995). Quantitative estimates of various climate parameters are obtained for fossil floras by ordinating the fossil leaf character states along with the CLAMP data set followed by further procedures to correlate the resulting axis scores with climate variables.

It would have been of great interest to compare the results of a CLAMP analysis with the climatic parameters obtained in this study. However, a CLAMP analysis was excluded primarily because of the problem of missing data in these Late Cretaceous Antarctic floras. Wolfe (1993) states that for MAT predictions a sample size of greater than 20 species is required and for precipitation estimates, more than 25 species. Although there are 30 morphotypes within the Hidden Lake Formation flora and 31 within the Santa Marta Formation flora, many of the CLAMP characters are preserved in fewer than 20 morphotypes within each flora. For example, leaf apices can only be scored using CLAMP definitions for 19 morphotypes of the Hidden Lake Formation flora and 18 morphotypes of the Santa Marta Formation flora. Leaf margins, on the other hand, are preserved in 28 of the Hidden Lake Formation flora morphotypes and 29 of the Santa Marta Formation flora morphotypes. Estimates of MAT using SLR models based on leaf margin styles are therefore considered more reliable for this study of palaeotemperatures on the Antarctic Peninsula during the Late Cretaceous.

It has also been argued that the simpler univariate leaf margin analysis approach is the most reliable and unambiguous method for determining palaeotemperatures. Wilf (1997) tested the leaf margin analysis and CLAMP procedures on modern floras from various latitudes and concluded that leaf margin analysis generally gave more accurate results. Wilf (1997) suggested that one of the inadequacies of the CLAMP (1993) database is the inclusion of extremely cold and dry sites, since under these conditions correlations between climate and leaf

physiognomy are known to be different (Wolfe 1979, 1993, Wing and Greenwood 1993, Gregory and McIntosh 1996). Wilf (1997) also noted that fewer numbers of species were used in comparison to the earlier leaf margin analysis study by Wolfe (1979). In CLAMP, the leaf margin character dominates the temperature signal and Wilf (1997) was unconvinced that additional characters could contribute much more information. One of the reasons given by Wilf (1997) for the greater reliability of leaf margin analysis was that the recording of some of the CLAMP characters is rather subjective. The nature of the leaf margin may be more consistently recorded by different researchers than some of the CLAMP characters, e.g. leaf basal style. Leaf margin analysis is also considered robust to the effects of taphonomic processes (Burnham 1994), unlike the CLAMP procedure, which incorporates characters of leaf size.

6.3.5.2 Multiple linear regression (MLR)

MLR models involve the use of more than one variable to predict climate parameters. Several workers have produced multiple linear regression models based on the CLAMP character set of Wolfe (1993) following studies of the significance levels of statistical correlation between leaf characters and climate parameters such as MAT and precipitation. It has been concluded that more accurate results might come from reducing the number of characters used in the analysis (Wiemann et al. 1998). One of the reasons given for this is the subjectivity of scoring the characters from the CLAMP data set. As stated above, there may be differences in the scoring of certain characters, e.g. leaf base, by different researchers (Wilf 1997). Using a smaller number of reliably scored characters may give better estimates of palaeoclimate parameters. Wiemann et al. (1998) also concluded that some characters are unimportant in climate prediction and removing these may also reduce errors.

Based on a subset of the CLAMP data set with sites experiencing extreme cold (cold month mean < -2.0°C) removed, Wing and Greenwood (1993) obtained regression equations to predict palaeoclimate parameters using from two to six characters. The CLAMP character list of 31 characters is subdivided into seven groups (lobing, teeth, size, apex, base, length/width ratio, and shape) (Wolfe 1993). Wing and Greenwood (1993) reduced the list of characters to more independent variables by selecting one character for each aspect of leaf form with low correlation with the other characters and high correlation with the climate parameter. In these models, power functions are used to transform data before it is entered. Wiemann et al. (1998) tested the reliability of various methods of determining MAT and precipitation using leaf physiognomy and derived their own MLR models from the CLAMP data set for temperate and tropical America and Japan. The study by Wiemann et al. (1998) on correlation coefficients between the CLAMP leaf characters and climate parameters demonstrated that leaf morphology has a stronger relationship with temperature than precipitation. MAT was most highly correlated with leaf margin characters and growing season precipitation (GSP) with length/width ratio, leaf shape, the presence of an attenuate apex, and leaf size. The Wiemann et al. (1998) model predicts GSP rather than MAP because the later version of the CLAMP database used does not include MAP, as winter precipitation is stated to be insignificant to plants in areas with a shorter

than 12 month growing season. Wiemann *et al.* (1998) proposed that with the use of power functions, small biases could leaf to large errors, so data is not transformed before it is entered into their equations. The MLR equations derived by Wing and Greenwood (1993) and Wiemann *et al.* (1998) are given in Table 6.12.

MLR	Source
MAT = 2.536 + 17.372(none) + 2.896(emarg) − 8.592(<1:1) r^2=0.863, s.e. = ±1.988°C	Wing and Greenwood (1993)
MAT = 9.865 + 0.207(none) − 0.058(Brnd) − 0.202(<1:1) r^2=0.898, s.e. = ±1.94688°C	Wiemann *et al.* (1998), M. Wiemann pers. comm.
MAP = 11.489 + 167.948(atten) + 377.735(mesoII) r^2=0.497, s.e. = ±57.967cm	Wing and Greenwood (1993)
GSP = 31.6 − 3.393(leptII) + 2.400(atten) − 2.671(Bcord) + 2.360(2-3:1) + 3.122(3-4:1) r^2=0.796, s.e. = ±48.22455cm	Wiemann *et al.* (1998), M. Wiemann pers. comm.

Table 6.12 Multiple linear regression models derived from CLAMP data sets (Wing and Greenwood 1993, Wiemann *et al.* 1998, M. Wiemann pers. comm.).

Abbreviations in parentheses refer to various features of leaf outline and size from the CLAMP character set: (none) − no teeth; (leptII) − leptophyll II; (mesoII) − mesophyll II; (atten) − attenuate apex; (emarg) − emarginate apex; (Bcord) − cordate base; (Brnd) − round base; (<1:1) − length/width ratio <1:1; (2-3:1) − length/width ratio 2-3:1; (3-4:1) − length/width ratio 3-4:1. In the equations of Wing and Greenwood (1993) the quantities indicated in parentheses represent the arcsines (in radians) of the square roots of the proportions of leaf taxa in an assemblage possessing the indicated characters. In the equations of Wiemann *et al.* (1998) the abbreviations in parentheses refer simply to the percentage of leaf types within a flora with the indicated characters.

The templates defining leaf size classes in the CLAMP character set (Wolfe 1993) are difficult to use for these fragmentary Late Cretaceous leaf fossils. In order to facilitate classification, the boundaries between the CLAMP size classes given by Wilf *et al.* (1998) were used in this study (Table 6.13).

CLAMP size classes	Area, A (mm²)
leptophyll I	A≤19
leptophyll II	19<A≤91
microphyll I	91<A≤392
microphyll II	392<A≤1420
microphyll III	1420<A≤3516
mesophyll I	3516<A≤6226
mesophyll II	A>6226

Table 6.13 CLAMP size boundaries measured from Wolfe (1993) by Wilf *et al.* (1998).

Results

In order to facilitate comparison of these Late Cretaceous fossils with other leaf records, the angiosperm leaves in this study were described and coded using terminology popular with palaeobotanists carrying out systematic work (Chapters 3, 4 and 5). There are subtle differences in the terminology and coding in a CLAMP analysis. For palaeoclimatic analysis, the leaf morphotypes of the Hidden Lake Formation and Santa Marta Formation floras were

reexamined and coded according to CLAMP definitions. Tables in Appendix 4 present the resulting data required for use in this study of Late Cretaceous climatic conditions on the Antarctic Peninsula. These data include morphotype size ranges (Table A4-1), apical styles (Table A4-2), basal styles (Table A4-3) and length/width ratios (Table A4-4). For each of the characters required for the equations in Table 6.12, the percentages of morphotypes within the Hidden Lake Formation and Santa Marta Formation floras possessing that character are given in Table 6.14. For each character, the percentage only takes into account those morphotypes in which that character is preserved.

Character	Hidden Lake Formation flora (%)	Santa Marta Formation flora (%)
(none)	54	62
(lobed)	10	10
(leptll)	0	0
(mesoll)	3	3
(atten)	53	44
(emarg)	4	3
(Bcord)	8	12
(Brnd)	17	12
(<1:1)	7	4
(2-3:1)	44	50
(3-4:1)	7	7

Table 6.14 Percentages of morphotypes within each flora displaying characters used in palaeoclimatic analysis.

More detailed information is given in Appendix 4.

Abbreviations in parentheses refer to various features of leaf outline and size from the CLAMP character set: (none) – no teeth; (lobed) – lobed; (leptll) – leptophyll II; (mesoll) – mesophyll II; (atten) – attenuate apex; (emarg) – emarginate apex; (Bcord) – cordate base; (Brnd) – round base; (<1:1) – length/width ratio <1:1; (2-3:1) – length/width ratio 2-3:1; (3-4:1) – length/width ratio 3-4:1.

Inputting the data from these Antarctic fossils (summarised in Table 6.14) into the equations outlined in Table 6.12 produces the estimates of temperatures and precipitation presented in Table 6.15.

MLR source	Hidden Lake Formation flora			Santa Marta Formation flora		
	MAT (°C)	MAP (cm)	GSP (cm)	MAT (°C)	MAP (cm)	GSP (cm)
Wing and Greenwood (1993)	15.2 ±2	214.2 ±58		17.1 ±2	199.1 ±58	
Wiemann et al. (1998), M. Wiemann pers. comm.	18.6 ±1.9		263 ±48.2	21.2 ±1.9		245 ±48.2

Table 6.15 Estimates of MAT, MAP and GSP for the Hidden Lake Formation and Santa Marta Formation floras calculated using MLR equations.

Both the MLR equations used to estimate precipitation utilise leaf size characters. Although attempts were made to reconstruct the sizes of fragmentary specimens to obtain maximum dimensions for each morphotype (Section 6.3.3), these measurements are still expected to be smaller than the actual maximum leaf sizes of the parent plants because of the effects of taphonomic processes (Chapter 7). This suggests that the calculated figures for MAP and GSP

given in Table 6.15 are minimum estimates of actual precipitation. In addition, three of the four MLR models given in Table 6.12 incorporate character state percentages based on apical styles. As stated above, apical forms could only be categorised for 19 of the Hidden Lake Formation flora morphotypes and 18 of the Santa Marta Formation flora morphotypes. It should be noted, therefore, that since apical character states cannot be defined for the minimum 20 taxa required for reliable palaeoclimatic interpretation (Wolfe 1993), the resulting estimates of precipitation based on the equations of both Wing and Greenwood (1993) and Wiemann *et al.* (1998) and the MAT estimate from the equation of Wing and Greenwood (1993) are regarded as highly tentative.

6.4 Summary of Results

Using the NLR approach, the climatic tolerances of examples of living angiosperm groups whose leaves show similarity to the Antarctic fossils studied here generally conjure a picture of a warm, moist and equable climate. However, the validity of extrapolating back these climatic conditions for the fossil floras is uncertain since the Late Cretaceous leaves cannot confidently be assigned to modern families or orders. The relatively high percentage of leaf morphotypes possessing attenuate apices within these floras is considered to reflect persistent humidity on the Antarctic Peninsula. Analysis of leaf size distribution according to the classification by Webb (1959) is indicative of temperate to subtropical environments and mesothermal temperatures. It is considered that the effects of taphonomic processes (Chapter 7) on leaf size data mean that the very low leaf size indices calculated cannot be used to infer a lack of moisture and the interpreted mean annual temperatures of 12°C for the Hidden Lake Formation flora and 11°C for the Santa Marta Formation flora are minimum estimates of actual temperatures. The proportions of morphotypes with lobed margins within both the Hidden Lake Formation and Santa Marta Formation floras are suggestive of mean annual temperatures of about 15°C.

The results from the application of leaf margin analysis, SLR and MLR models are summarised in Table 6.16.

Model	Hidden Lake Formation flora			Santa Marta Formation flora		
	MAT (°C)	MAP (cm)	GSP (cm)	MAT (°C)	MAP (cm)	GSP (cm)
LMA – Northern Hemisphere (Wolfe 1979)	18.0 ±1.8			20.7 ±2.1		
LMA – Southern Hemisphere (Wolfe 1979)	16.3 ±1.6			18.3 ±1.8		
SLR (Wolfe 1979, Wing and Greenwood 1993)	17.7 ±0.8			20.1 ±0.8		
SLR (Greenwood 1992, Wiemann et al. 1998)	16.3			18.0		
SLR (Wilf 1997)	17.7 ±2.0			20.0 ±2.0		
SLR – CLAMP (Wilf 1997)	15.5 ±3.4			17.8 ±3.4		
SLR – CLAMP with cold sites excluded (Wilf 1997)	16.4 ±2.1			18.4 ±2.1		
SLR – CLAMP large leaves (Wilf et al. 1998)		109.3			67.3	
SLR – Leaf area analysis (Wilf et al. 1998)		77.2 -23.3 +33.3			95.6 -28.8 +41.3	
SLR – Large leaves (Wilf et al. 1998)		59.4			59.1	
MLR – Wing and Greenwood (1993)	15.2 ±2	214.2 ±58		17.1 ±2	199.1 ±58	
MLR – Wiemann et al. (1998)	18.6 ±1.9		263 ±48.2	21.2 ±1.9		245 ±48.2

Table 6.16 Summary of data on palaeoclimatic variables obtained for the Hidden Lake Formation and Santa Marta Formation floras using leaf margin analysis (LMA), SLR and MLR models.

The standard errors for the leaf area analysis SLR of Wilf et al. (1998) are asymmetrical because they are converted from logarithmic units.

The results from the application of leaf margin analysis, SLR and MLR models summarised in Table 6.16 suggest mean annual temperatures of approximately 12-21°C for the Hidden Lake Formation flora and 14-23°C for the Santa Marta Formation flora. Although temperatures for the Santa Marta Formation assemblage are generally higher than those for the Hidden Lake Formation, there is considerable overlap in the ranges and so there is no discernable difference between the signals from the two floras.

The lowest temperature estimates were obtained from the SLR equation based on the complete CLAMP data set derived by Wilf (1997). The standard errors are greater for this model and the inclusion of extremely cold sites (cold month mean (CMM) < -2°C) in the CLAMP database has been shown to produce cooler MAT estimates (Wing and Greenwood 1993, Gregory and McIntosh 1996, Wilf 1997). In regions where the cold month mean falls below -2°C, prolonged winter freezes are common and the relationship between climate and leaf physiognomy is known to be different (Wolfe 1979, 1993, Wing and Greenwood 1993). It is for this reason that several workers (e.g. Wing and Greenwood 1993, Gregory and McIntosh 1996, Wilf 1997) have derived SLR and MLR models from the CLAMP data set with the sites experiencing a cold month mean of less than -2°C removed. In contradiction, the highest estimates of MAT on the Antarctic Peninsula during the Late Cretaceous were provided by the Wiemann et al. (1998)

MLR, in which all sites within the CLAMP data set were used to derive the model. It has been proposed that excluding the extremely cold sites leads to significantly better models with reduced standard errors (Gregory and McIntosh 1996). Removing the temperature estimates based on the complete CLAMP data set in this study reduces the range of MATs slightly to 13-20°C for the Hidden Lake Formation flora and 15-23°C for the Santa Marta Formation flora. However, in the testing of various SLR and MLR models on modern vegetation in Florida by Wiemann *et al.* (1998), of the methods used in this Antarctic study the estimate closest to actual MAT for one of the sites was given by the Wiemann *et al.* (1998) MLR equation. Therefore, the final MAT estimates provided in this study of Late Cretaceous climatic conditions on the Antarctic Peninsula incorporate all the results summarised in Table 6.16.

The results from the application of SLR and MLR equations summarised in Table 6.16 provide estimates of mean annual precipitation of 54-272cm for the Hidden Lake Formation flora and 59-257cm for the Santa Marta Formation flora. The Wiemann *et al.* (1998) model predicts growing season precipitation of 215-311cm for the Hidden Lake Formation flora and 197-293cm for the Santa Marta Formation flora. The overlap in the range of precipitation estimates means that no difference between the two Late Cretaceous assemblages can be detected. For comparison, the lowest precipitation estimates are typical of open canopy woodland at high altitudes in Payson, Arizona, (where the MAT is about 13°C) and the highest precipitation estimates are similar to those observed in the lower montane wet forests of Puerto Rico (where the MAT is approximately 22°C) (meteorological data from Wolfe 1993).

The highest estimates of precipitation result from the application of MLR models. In the comparison of actual and predicted amounts for modern vegetation samples by Wiemann *et al.* (1998), the closest estimates were provided by the Wing and Greenwood (1993) MLR equation. However, the precipitation predictions from the application of MLR models in this study are highly tentative because these equations include the apical form character which cannot be coded for the minimum 20 taxa required for reliability. The lowest estimates are given by the SLR equations which use only leaf size to predict precipitation. The leaf size distribution is considered to be strongly affected by taphonomic biases in these fossil floras (Chapter 7) and thus these precipitation estimates are considered to reflect minimum amounts of actual precipitation on the Antarctic Peninsula during the Late Cretaceous.

Using the techniques outlined above, a picture of a warm climate with no extended freezing periods and adequate moisture is proposed for the Coniacian-Santonian of the Antarctic Peninsula. A comparison of these results with palaeoclimatic interpretations from other sources is presented in Chapter 7.

7   Discussion of the palaeoecological implications of these Late Cretaceous angiosperm leaf floras

This chapter brings together results and interpretation from previous chapters and discusses the wider relevance of the main components of this study. The floral composition and palaeoclimate of the Antarctic Peninsula area during the deposition of the Hidden Lake Formation (Coniacian) and Santa Marta Formation (Santonian-early Campanian) are discussed with a consideration of the taphonomic biases that might have affected the two Late Cretaceous assemblages studied.

7.1 Taphonomic interpretation and discussion

This study of angiosperm leaves aims to provide new information on the composition of the Late Cretaceous Antarctic Peninsula vegetation and the palaeoclimate under which it grew, but the taphonomic biases operating on this marine fossil assemblage must be considered.

7.1.1 Implications of taphonomic bias for this study of Late Cretaceous angiosperm leaf flora composition

In Chapter 5 the architectural characteristics of leaf morphotypes within the Hidden Lake Formation and Santa Marta Formation floras were described. The comparisons drawn with fossil and living angiosperm leaves are discussed in Section 7.2. However, the composition of these Late Cretaceous Antarctic fossil assemblages is affected by taphonomic bias.

One of the strongest controls on the composition of a fossil assemblage is considered to be the proximity of the source vegetation. It is assumed that leaves tend to be deposited relatively close to their source and that fossil assemblages best represent the immediate flora, with the most abundant fossil taxa reflecting the dominant taxa growing close to the site of deposition (Greenwood 1991, 1992). The fossil record is biased toward species from lowland and wetland environments where conditions favour preservation, although there may be slightly elevated land inhabited by hinterland taxa within these environments (Ferguson *et al.* 1999). The leaves preserved within the shallow marine strata of the James Ross Basin may therefore represent plants growing on the delta top close to the shore.

Studies of modern deltas by Spicer (1981) and Gastaldo (1986) suggest that leaves transported as suspended load may remain recognisable for months and that leaves entering river flow may be less likely to decay and be fragmented by tide action than litter from the most proximal deltaic environments. So it is also possible that these Late Cretaceous leaves were transported to the delta front via river channels. Following a study of leaf deposition in the paratropical rain forests of Guatemala, Burnham (1989) assumed that only leaves from overhanging plants enter river channels and that streamside species are over-represented in fossil floras. Certain species may be concentrated along the edge of rivers because of adaptations to moisture, light and dispersal phenomena. Shrubs and herbs are abundant, away from the dense cover of the

canopy, and species heterogeneity increases away from river channels (Burnham 1989). This implies that these Antarctic collections may be dominated by species adapted to life along the edge of watercourses. However, modern studies have shown that riparian elements extend deeper into the forest in more humid climates (Ferguson et al. 1999). Moderately high rainfall in the high latitudes during the Late Cretaceous is indicated by the abundance of coals deposited (Francis and Frakes 1993), suggesting that fossil assemblages of streamside vegetation may give a better representation of the local flora than during other periods.

Burnham (1989) attempted to quantify taphonomic biases through studies of modern fluvial litter samples. It was expected that the immediate flora would dominate litter samples. However, Burnham (1989) demonstrated that although forest composition may vary along and around a river, litter samples from different sites along the channel are composed of relatively low diversity homogenous vegetation. This reflects not only the strong homogeneous signal of plants adapted to life along the water's edge, but also considerable mixing of leaves from different plants growing at distant sites along the river (Burnham 1989). During the Late Cretaceous, the Antarctic Peninsula was a high relief active volcanic island arc and it is possible that there is a mixing of leaves from plants growing at various altitudes in different local climates.

Studies of modern vegetation have also indicated that plants with compound leaves may be over-represented. Burnham (1989) gave two reasons for this:

- Compound leaves have a higher chance of representation because they break up into numerous leaflets.
- Taxa with compound leaves may show an ecological preference for the water's edge environment.

There are no compound leaves preserved amongst these transported and fragmented leaf fossils. One method that has been used to identify possible isolated leaflets from compound leaves is the possession of an asymmetrical leaf base (Dilcher 1974). The leaf bases are not preserved in all of the specimens, but from those present, 69% of the Hidden Lake Formation leaves and 44% of the Santa Marta Formation leaves show asymmetrical bases (see Table 3.1). This may support the presence of a taphonomic bias towards streamside species in the Hidden Lake Formation flora, but it is possible that the ecological preference for habitats along water courses exhibited by modern plants with compound leaves, such as legumes, may not yet have evolved in the Cretaceous.

An indication of the taphonomic bias towards streamside vegetation may also be obtained from a study of lamina form, since narrow leaves are more common in these environments (Spicer 1990a). The data illustrated in Figure 2.8 shows that average length/width ratios for both floras are between 1.4:1 and 1.9:1. Leaves with these ratios would not be considered narrow (Hickey 1979), but as outlined above, many of these leaves are fragmentary. Following the grouping of leaves into morphotypes (Chapter 4), it was possible to obtain estimates of the length/width ratios of each morphotype from the best preserved specimens. These results are presented in

Appendix 4, Table A4-4 and Figure 7.1. These estimates suggest that almost half of the leaves within the Hidden Lake Formation had original length/width ratios of at least 2:1, while the proportion is two thirds for the Santa Marta Formation leaves. This may indicate that the Antarctic Peninsula assemblages are biased towards narrow-leaved streamside vegetation.

Length/width ratios
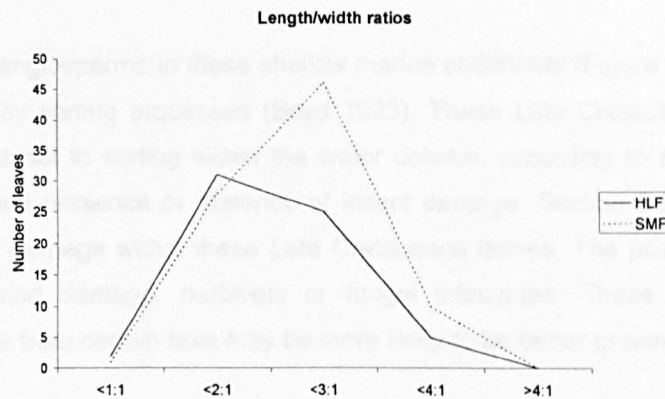
Figure 7.1 Length/width ratios for the leaves of the Hidden Lake Formation and Santa Marta Formation floras.

The preservation of the Hidden Lake Formation leaf flora in one horizon within deltaic sediments may reflect some catastrophic event, possibly related to flooding and storms with strong winds. There may therefore be a mixture of juvenile and mature foliage which may be assigned to separate taxa because of variations in venation patterns, (e.g. modern *Eucalyptus* leaves do not have an intramarginal vein when immature (Pole 1991)), possibly resulting in an overestimation of diversity. This may also account for the large range in leaf sizes observed in these floras (see Section 2.5.3).

Figure 2.1 and Figure 2.2 clearly show that angiosperm remains are dominant within these Late Cretaceous floras, but this does not necessarily imply that angiosperms were dominant within the source vegetation. There may be a bias towards representation of leaves from deciduous species. It is expected that there will be more leaves from woody dicotyledonous angiosperms with synchronous leaf abscission than evergreen or herbaceous plants (Burnham 1989, Ferguson *et al.* 1999). The occurrence of relatively large well-preserved leaf floras in marine sediments might reflect a seasonal bias in species composition towards the synchronous leaf fall from deciduous species. The Hidden Lake Formation deltaic sediments are considered to have formed relatively rapidly. Through comparison with the study of leaf preservation by Jefferson (1982b), the high curvature of the surfaces on which these leaf fossils are preserved suggests that these sediments were deposited rapidly in a low energy current regime. Seasonal bias may therefore have had an effect on the species preserved. The fossil leaves preserved may represent leaf fall from one growing season. This may account for the dominance of angiosperm leaves, the lack of conifer remains and the relatively high proportion of fern foliage entering the water column on death (Figure 2.1). In contrast, the younger Santa Marta Formation represents quieter more offshore marine conditions (Table 1.3) and elements of the flora are more widely distributed geographically (Figure 1.2). Slower rates of deposition may

indicate that this flora is less affected by seasonal patterns and perhaps seasonally deciduous leaves are not so dominant, with an increased proportion of conifer remains in this collection (Figure 2.2). The inferred strong preservational bias affecting angiosperm frequency in these Antarctic floras is considered to hinder any comparative work on biodiversity based on palynological assemblages such as that by Drinnan and Crane (1990).

The abundance of angiosperms in these shallow marine sediments (Figure 2.1, Figure 2.2) may also be explained by sorting processes (Boyd 1993). These Late Cretaceous Antarctic floras may have been subject to sorting within the water column, according to size, density, shape, stomatal density, and presence or absence of insect damage. Section 2.5.1 outlines possible pre-abscission leaf damage within these Late Cretaceous leaves. The possible causes of this damage include wind damage, herbivory or fungal infestation. These processes may be selective and leaves from certain taxa may be more likely to be better preserved than others.

The degree of fragmentation and levels of preservation of the leaves from the Hidden Lake Formation and Santa Marta Formation floras are illustrated in Figure 2.4, Figure 2.5, Figure 2.6, Figure 2.7. Fragmentation of fossil leaves usually occurs during bedload transport or tidal agitation (Gastaldo 1986, Gastaldo *et al.* 1996). During transport the leaves were subjected to abrasion, disarticulation and decay. The degradation observed in the less well preserved leaves has made the classification of the leaves into different species very difficult. Many of these leaves are impossible to identify, since diagnostic characteristics are often not clearly preserved. However, there are excellently preserved almost whole leaves and once partitioned into separate morphotypes, more fragmentary specimens could then be placed within the most similar morphotype (see Chapter 4). There is an element of bias in the leaf taxa established in this study in that different species may have different decomposition rates and the leaves of certain species may be more easily fragmented than those of others (Burnham 1989). There is a low proportion of palmately lobed leaves. Only 2% of the Hidden Lake Formation leaves and 5% of the Santa Marta Formation leaves possess lobed margins (see Chapter 3). Palmately lobed leaves are considered abundant in floras of this age from other areas (Hickey and Doyle 1977) and are suggested typical of riparian floras, so the rarity of lobed forms identified in these Antarctic floras may well be due to taphonomic biases.

In summary, these Late Cretaceous isolated and fragmentary leaves preserved within marine sediments clearly form allochthonous assemblages. The best preserved leaves within these floras and the morphotypes established are probably representative of certain species that are most resistant to pre-abscission damage, fragmentation and decay. Sorting within the water column may account for the abundance of angiosperm leaves and may have resulted in increased proportions of particular taxa. The floras are more likely to represent woody deciduous dicotyledonous angiospermous trees or shrubs, which produce greater numbers of leaves. The preservation of large leaf collections in marine sediments may also represent some catastrophic event, and the resultant mixture of juvenile and mature leaves may lead to an overestimation of diversity. The species present are likely to be those growing in those localities

on the Antarctic Peninsula closest to the preservation sites and therefore the fossil floras probably reflect a lowland plant community. The floras are likely to represent plants inhabiting the delta top and homogeneous streamside vegetation with a mixture of leaves from plants growing at various points along river channels.

7.1.2 Implications of taphonomic bias for the interpretation of Late Cretaceous palaeoclimatic conditions

In Chapter 6 several different approaches were used to interpret palaeoclimatic conditions on the Antarctic Peninsula during the Late Cretaceous. These methods include comparison with possible nearest living relatives, leaf margin analysis, examination of apical styles, assessment of leaf size distributions and application of simple linear regression and multiple linear regression models. The results are compared with previously published palaeoclimatic inferences in Section 7.3. However, the floral composition and leaf physiognomy within these fossil assemblages are strongly affected by taphonomic bias, which is an important consideration in the determination of palaeoclimate parameters.

The previous section on taphonomic implications for floral composition outlines the many biases which suggest that these Late Cretaceous fossil assemblages provide an incomplete picture of the parent plant community. Although there is an increased preservation potential of plant species growing in lowlands and along watercourses, modern studies (e.g. Ferguson et al. 1999) suggest that under the inferred moderately high rainfall in the Late Cretaceous high latitudes (Francis and Frakes 1993) riparian elements may have inhabited wider areas and may be more representative of the local flora. However, this bias along with the possible overrepresentation of taxa with compound leaves, bias towards plant groups with the deciduous habit, sorting processes within the water column, selective pre-abscission damage (e.g. herbivory), easier fragmentation of some leaf forms (e.g. palmately lobed leaves) than others, differential decomposition rates, and abrasion, disarticulation and decay during transport hindering identification all cause difficulties in the extrapolation of climatic conditions from the tolerances of possible nearest living relatives.

These taphonomic biases also have implications for the determination of palaeoclimate parameters using leaf physiognomy. Palaeoclimate interpretations should be based on the regional climax vegetation, but there is only likely to be a small percentage of the regional vegetation preserved within the shallow marine depositional environment of the Hidden Lake Formation and Santa Marta Formation fossils. As stated above, these floras instead probably represent elements of disturbed delta top and streamside vegetation growing on the active volcanic arc. The vegetation of disturbed habitats (particularly streamside) exhibits higher proportions of species with toothed margins (Wolfe and Upchurch 1987). The estimates of Late Cretaceous temperatures based on leaf margin analysis and SLR and MLR equations incorporating marginal characters are therefore likely to be minimum estimates of actual mean annual temperatures.

It was suggested in Section 7.1.1 that the preservation of these leaf collections in marine sediments might be indicative of some catastrophic event. Conditions on this active volcanic arc may not have allowed the development of climax vegetation. The leaf physiognomic characters of successional vegetation may not be in tune with current environmental conditions (Wolfe and Upchurch 1987) and thus temperature and precipitation values derived from this study of leaf size and form may be unreliable. In addition, catastrophic events such as flooding and storms may have resulted in the preservation of a mixture of mature and juvenile leaves assigned to separate taxa. The analysis of leaf size distribution to determine palaeoclimate parameters should not utilise juvenile foliage (Webb 1959), so this may be one taphonomic factor producing an underestimate of leaf size indices and a corresponding underestimation of climatic conditions.

Riparian vegetation tends to demonstrate distinctive leaf morphology (e.g. higher length/width ratios) (Spicer 1989, 1990a,b). The work on modern vegetation samples by Wolfe (1993) demonstrates that overrepresentation of streamside species does not reduce the reliability of temperature estimates based on leaf physiognomy. However, Wolfe's (1993) taphonomic studies indicate that the bias towards fluviatile elements in fossil assemblages may lead to leaf physiognomy based predictions of wetter than actual conditions. It is possible that there is a bias towards narrow leaves from streamside environments in the Hidden Lake Formation and Santa Marta Formation floras (Figure 7.1). This is an important consideration in this study because length/width ratios are used in the MLR model of Wiemann *et al.* (1998) to predict GSP and may contribute towards an overestimation of precipitation. However, Burnham (1989) suggested that there might be an ecological preference of small-leaved taxa for habitats along watercourses. This may contribute to an underestimation of leaf sizes. In palaeoclimatic interpretation, leaf size is generally used as a signal of relative humidity (Wolfe and Upchurch 1987) and therefore this bias may result in lower estimates of precipitation than were actually experienced on the Antarctic Peninsula during the Late Cretaceous. As outlined in Section 7.1.1, the water's edge is inhabited by relatively low diversity homogeneous vegetation (Burnham 1989). It is therefore considered that these biases are reduced by the requirement of a minimum of 20 taxa for accurate predictions of palaeoclimatic parameters provided by leaf margin analysis, SLR and MLR models (Wolfe 1993). However, in this study of Late Cretaceous climates, apical style (which is an important predictor of precipitation in the MLR equations applied) is preserved in only 19 morphotypes in the Hidden Lake Formation flora and 18 in the Santa Marta Formation flora. The precipitation estimates provided by this study are therefore regarded as highly tentative. A significant problem in the interpretation of these fossil assemblages is the probable mixing of leaves from plants growing at distant sites along rivers within the water column, as observed in the modern environment by Burnham (1989). These floras may represent an accumulation of leaves from plants growing at various altitudes and in different local climates on the high relief volcanic arc.

The leaf size distribution within a flora is one of the most important predictors of precipitation (Wiemann *et al.* 1998), although it has also been correlated with mean annual temperatures

(Greenwood 1992). The SLR and MLR equations applied in this study use leaf morphotype sizes to calculate precipitation figures for the Late Cretaceous Antarctic Peninsula. The leaf specimen sizes of both floras are all rather small (Figure 2.8, Figure 2.9). Studies of taphonomic processes operating in modern environments (e.g. Spicer 1981, Ferguson 1985, Gastaldo et al. 1996, Bateman 1999) indicate that there are several possible biases acting on the leaf floras producing an underestimate of leaf size. The leaves with the greatest potential for preservation are those growing in the parts of the forest subject to the highest wind speeds, from tall emergent trees, canopy layers, and along the margin of the forest (Gastaldo et al. 1996, Ferguson et al. 1999). These trees also tend to contribute more to leaf litter because they possess bigger crowns (Greenwood 1992, Ferguson et al. 1999). Outer 'sun' leaves growing higher in the canopy are more likely to be preserved in a marine basin than 'shade' leaves, which tend to accumulate close to the plant. 'Sun' leaves are exposed to stronger sunlight and are smaller and thicker than 'shade' leaves. However, only 'sun' leaves should be used in the characterisation of leaf size distribution (Webb 1959).

The smaller leaves on a tree are also more likely to be transported to the marine basin because they are subject to sorting within the water column. With increased transport, the number and size of plant parts decreases (Spicer 1981, Ferguson 1985, Gastaldo et al. 1996). The fragmentation observed in these fossil leaves (Figure 2.4, Figure 2.7) confirms that the leaf sizes of the Cretaceous floras studied are minimum estimates of the leaf sizes in the source vegetation. In order to compensate for the fragmentation of the leaves during transport, attempts were made to reconstruct the original shapes and sizes of these fossil leaves. The maximum estimated size of each morphotype within the Hidden Lake Formation and Santa Marta Formation floras was used in the palaeoclimatic analyses (Chapter 6) in an attempt to reduce taphonomic bias. Despite this, the maximum leaf morphotype sizes are still probably not representative of the actual leaf size distribution within the source vegetation, resulting in minimum estimates of precipitation on the Antarctic Peninsula during the Late Cretaceous.

There may also be preferential fragmentation of thinner leaves with toothed margins (Wolfe 1993). The inclusion of fragmentary specimens within the analyses is believed to considerably reduce this bias. The nature of a leaf margin is readily recognised, even in very fragmentary specimens. It has been suggested that the interpretation of mean annual temperatures using margin characteristics is robust to taphonomic processes (Burnham 1989).

In summary, taphonomic bias and levels of preservation hindering certain identification of these Late Cretaceous angiosperm leaves means that interpretation of palaeoclimatic conditions using the nearest living relative approach is unreliable. The accuracy of temperature and precipitation estimates derived from foliar physiognomic methods is also reduced by taphonomic processes. The figures obtained for MAP and GSP on the Antarctic Peninsula during the Late Cretaceous are highly tentative. The tendency towards incomplete preservation of leaf apices means that MLR equations do not provide reliable precipitation estimates. A possible overrepresentation of streamside species may also have resulted in increased

proportions of narrow leaves and an overestimation of precipitation from MLR models. However, leaf size is one of the most important predictors of precipitation and there are several factors producing an underestimation of leaf size. These include catastrophic events leading to the deposition of juvenile foliage, a possible ecological preference of small-leaved taxa for the water's edge environment, a bias towards the preservation of 'sun' leaves, and sorting and fragmentation within the water column. Although attempts were made to compensate for some of these factors, it is considered that precipitation estimates provided by SLR equations are minimum estimates of actual precipitation on the Antarctic Peninsula during the Late Cretaceous. Mean annual temperature estimates based on leaf margin characters are generally considered robust to taphonomic processes. The estimates of temperatures on the Antarctic Peninsula during the Late Cretaceous are therefore provided with some confidence. However, the possibility that the fossil assemblages do not represent climax vegetation may mean that both temperature and precipitation estimates are unreliable because leaf physiognomic characters are not in tune with the environment. A further complication is the probability that these Late Cretaceous floras are an accumulation of leaves from plants growing at various altitudes in different local climates on the high relief volcanic arc.

7.2 Comparison of the results of this study with published records of Late Cretaceous vegetation on the Antarctic Peninsula

In this section, the results from this study of Coniacian-Santonian angiosperm leaf fossils are combined with other data from leaves, pollen, wood, and cuticle remains in order to construct a picture of the changing composition of the Antarctic Peninsula vegetation during the Cretaceous and into the Tertiary. Askin (1992) presented a compilation of all the previously published fossil plant information. In the light of more recently published evidence and results from this project, an updated version of this chart is presented here (Figure 7.2). As in this study, many of the previously recorded occurrences of angiosperm families are not always confidently established, but often are simply a suggestion of the modern angiosperm family bearing similar features to the fossils studied in each case. This is particularly the case for the earliest Albian records, where possible affinities with several modern families were proposed (Cantrill and Nichols 1996).

The most detailed previous work on Antarctic floras has been on the microfloras (e.g. Dettmann and Thomson 1987, Baldoni and Medina 1989, Baldoni 1992, Keating 1992, Askin 1992). More extensive work on the fossil angiosperm wood is only now being undertaken (e.g. Poole and Francis 1999, 2000, Poole et al., in press a,b). There have been relatively few detailed studies on fossil angiosperm leaves from the Cretaceous of the Antarctic Peninsula. The results from this study have been added to Figure 7.2.

Most of the angiosperm families considered similar to the leaves in this study have already been recognised on the Antarctic Peninsula but these new leaf records frequently extend the ranges.

Angiosperm Family	Cretaceous							Tertiary		
	late Alb	Cen	Tur	Con	Sant	Camp	Maas	Pal	Eoc	Olig
?Actinidiaceae										
?Anacardiaceae										
?Annonaceae										
Aquifoliaceae										
Araliaceae										
?Aristolochiaceae										
Atherospermataceae										
Bombacaceae										
?Canellaceae										
Casuarinaceae										
Chloranthaceae										
Bixaceae										
Cunoniaceae										
?Cruciferae										
?Dilleniaceae										
Droseraceae										
Elaeocarpaceae										
Epacridaceae										
Ericaceae										
?Fabaceae										
Gunneraceae										
?Hernandiaceae										
?Himantandraceae										
Illiciaceae										
Lauraceae										
?Leguminoseae										
Loranthaceae										
?Melastomaceae										
Menispermaceae										
Monimiaceae										
?Moraceae										
Myricaceae										
Myrtaceae										
Nothofagaceae										
Olacaceae										
?Pedaliaceae										
?Piperaceae										
Proteaceae										
?Rhamnaceae										
Sapindaceae										
Saxifragaceae										
?Saururaceae										
Sterculiaceae										
?Trimeniaceae										
Ulmaceace										
?Verbeniaceae										
Winteraceae										

—   Askin 1992

—   updated information

☐   examples of plant groups sharing diagnostic characters with the morphotypes in this study

Figure 7.2 Compilation of the results of this study with previously published reports of angiosperm fossils from the Late Cretaceous and Tertiary of the Antarctic Peninsula.

(Updated from Askin 1992, with added information from Dusén 1908, Czajkowski and Rösler 1986, Tanai 1986, Dettmann and Thomson 1987, Birkenmajer and Zastawniak 1989a, Li and Shen 1989, Rees and Smellie 1989 Chapman and Smellie 1992, Baldoni 1992, Cao 1992, 1994, Keating 1992, Askin 1994, 1997, Li 1994, Martin 1994, Torres et al. 1994, Askin and Jacobson 1996, Cantrill and Nichols 1996, Dutra et al. 1996, 1998, Dutra 1997b, 1998, Vizcaino et al. 1997, Hathway et al. 1998, Poole and Francis 1999, 2000, Poole et al., in press a,b, Poole and Francis pers. comm.)

7.2.1 Support from previously reported floras for the possible botanical affinities suggested for these Late Cretaceous angiosperm leaves

- Although previous records of cunoniaceous leaves from the Tertiary of King George Island (Dusén 1908, Czajkowski and Rösler 1986) are now considered more similar to the Proteaceae (Li 1994), there are Tertiary palynological records on the Antarctic Peninsula (Askin 1992). There is particular support for the presence of cunoniaceous leaves within the Hidden Lake Formation and Santa Marta Formation floras from fossil wood. Cunoniaceous wood has been reported from strata with a probable age range of Cenomanian to early Campanian from Livingston Island and the James Ross Basin (Chapman and Smellie 1992, Poole *et al.*, in press a).

- Fossils of the Myrtaceae of Late Cretaceous to Tertiary age on the Antarctic Peninsula include leaves, pollen and cuticle. The occurrence of a myrtaceous leaf form within the Santa Marta Formation flora is not unexpected. Palynological analysis of the Santa Marta Formation has recovered pollen assigned to the Myrtaceae (Baldoni 1992) and Zastawniak (1994) reported leaves with suggested affinities to the Myrtaceae from rocks of a similar age on King George Island.

- Lauralean fossils are a common component in many of the Late Cretaceous and Tertiary fossil assemblages from the Antarctic Peninsula, including leaves, cuticle and wood. The lack of palynological evidence is thought to be due to the low preservational potential of the pollen from this family (Drinnan *et al.* 1990, Cantrill and Nichols 1996). Apart from a leaf called Form D from strata with a probable age range of Cenomanian-Campanian on Livingston Island (Rees and Smellie 1989), the earliest records of lauraceous fossils on the Antarctic Peninsula are Santonian-Campanian leaves and wood (Zastawniak 1994, Poole *et al.*, in press b).

Other angiosperm families sharing diagnostic characters with the morphotypes in this study include:
- Nothofagaceae
- Sterculiaceae
- Elaeocarpaceae
- Atherospermataceae
- Annonaceae

If the affinities suggested by leaf architectural features can be confirmed, then these records from the Hidden Lake Formation and Santa Marta Formation floras would extend the ranges of these families (Figure 7.2).

The first angiosperms in Antarctica were herbaceous or shrubby chloranthaceous taxa (Hill and Scriven 1995), but no leaf forms similar to the leaves of modern Chloranthaceae were recognised.

The results from this study of Late Cretaceous Antarctic floras offer support to Dettmann's (1989, 1992) theories of evolution and dispersal of particular angiosperm families in the Southern Hemisphere. Some angiosperms, e.g. *Nothofagus*, may have originated in the Patagonia-Antarctic Peninsula area. The Coniacian-Santonian leaf forms showing similarities to *Nothofagus* may represent the earliest occurrences of this family or an ancestral group. Palynological or cuticular studies from the Hidden Lake Formation are required to confirm the identification of these early forms as *Nothofagus*, but the similarity of these leaves to modern species may offer support to the theory that the Nothofagaceae evolved in West Antarctica (Dettmann 1989, 1992). The disturbed volcanic environment and probable open canopies of these high latitude forests may have provided the conditions *Nothofagus* requires to regenerate (Hill and Scriven 1995).

The Antarctic Peninsula is believed to have acted as a dispersal corridor between east and west Gondwana during the Late Cretaceous. Hill and Scriven (1995) considered that the angiosperms migrated into and across Antarctica via several pathways, some from the east via Australia and some via South America. The presence of a morphotype sharing diagnostic characteristics with myrtaceous leaves within the Santonian Santa Marta Formation flora offers support for the migration of the Myrtaceae from Northern Gondwanan regions such as Gabon and Borneo in the Senonian through South America and the Antarctic Peninsula to arrive in East Antarctica, Australia and New Zealand during the Paleocene (Dettmann 1989), rather than an alternative route into Australia from the north (Hill and Scriven 1995). None of the fossils studied were found to show similarities to modern or fossil leaves referred to the Proteaceae, which may also support the idea of the evolution of this family around southern Australia and eastern Antarctica in the Campanian and its migration in the opposite direction (Dettmann 1989).

7.3 Palaeoclimate of the Late Cretaceous Antarctic Peninsula

The results of several different approaches to determine palaeoclimatic conditions on the Antarctic Peninsula during the Late Cretaceous were presented in Chapter 6. These methods include comparisons with possible nearest living relatives, analysis of leaf margins and leaf sizes, and the application of simple linear regression and multiple linear regression models.

These Late Cretaceous leaf morphotypes cannot confidently be assigned to orders or families, but the climatic tolerances of examples of plant groups with which the morphotypes share leaf architectural characteristics were provided for comparison with the palaeoclimatic predictions based on leaf physiognomy. The presence of leaf forms showing similarity to the Sterculiaceae, Lauraceae, Elaeocarpaceae, Atherospermataceae, Cunoniaceae and Myrtaceae suggests that the climate may have been warm and moist. However, there are also leaves similar to those from plants considered more representative of cool temperate climates (e.g. Nothofagaceae, Winteraceae). One possible explanation for the coexistence of plants with apparently different thermal requirements is that trees and shrubs of taxa similar to the Lauraceae, Sterculiaceae, Elaeocarpaceae and Annonaceae grew in the lowlands, while forms similar to Nothofagaceae and Winteraceae lived under different local climate conditions at higher altitudes. Since during the Late Cretaceous the Antarctic Peninsula region was an active volcanic island arc, it is likely that there were steep slopes allowing the development of different vegetation types in a relatively small geographic area. A similar conclusion was reached for the Santonian-Campanian flora of King George Island by Zastawniak (1994) who suggested that magnoliaceous-laurophyllous evergreen rain forests grew on lower slopes and at the foot of volcanoes, while *Nothofagus* and podocarpaceous conifers inhabited the higher altitudes.

According to the classification of Webb (1959), the leaf size distribution observed in these Late Cretaceous floras is typical of temperate or subtropical lowland and subtropical or tropical montane regions. Following an assessment of leaf size classes within an angiosperm flora from the Santonian-Maastrichtian of King George Island, Zastawniak (1994) described similar conditions of lower montane and lowland subtropical rain forests. The poor preservation of leaf margins prohibited quantitative estimation of temperatures using leaf margin analysis. However, through comparison with the study of Late Cretaceous climates by Wolfe and Upchurch (1987), a leaf size index of approximately 28 for the King George Island flora was considered to reflect a subhumid mesothermal climate (Zastawniak 1994). The leaf size index values of 8 and 10 for the morphotypes of the Hidden Lake Formation and Santa Marta Formation floras, respectively, are very low in comparison to those given for other Late Cretaceous floras. It is considered that the effects of taphonomic processes on leaf size data (Section 7.1.2) mean that the very low leaf size indices calculated are lower than the actual values for the parent vegetation and cannot be used to infer a lack of moisture. Table 6.14 summarises the percentages of morphotypes within the Hidden Lake Formation and Santa Marta Formation floras displaying characters of use in palaeoclimatic studies. A high percentage of the morphotypes (HLF 53%, SMF 44%) possess attenuate apices, but emarginate apices are observed in only a very small

percentage of leaf forms (HLF 4%, SMF 3%). The relatively high proportion of these Antarctic leaf morphotypes possessing attenuate apices is considered to reflect persistent humidity on the Antarctic Peninsula during the Late Cretaceous.

Estimates of precipitation were made using simple and multiple linear regression models. The SLR models are based only on leaf size, while the MLR models also take length/width ratios and apical and basal styles into account. These equations provided mean annual precipitation estimates of 54-272cm for the Hidden Lake Formation flora and 59-257cm for the Santa Marta Formation flora, as well as growing season precipitation estimates of 215-311cm for the Hidden Lake Formation flora and 197-293cm for the Santa Marta Formation flora. However, these precipitation predictions are highly tentative. The MLR equations include the apical form character which cannot be coded for the minimum 20 taxa required for reliability. Effects of taphonomic bias on length/width ratios and leaf size distribution (Section 7.1.2) also introduce errors. Therefore, the highest estimates of precipitation (resulting from the MLR models) are considered unreliable, but the lowest estimates (derived from SLR models) are considered to reflect minimum amounts of actual precipitation on the Antarctic Peninsula during the Late Cretaceous. Most previous palaeobotanical interpretations have provided estimates of high rainfall on the Antarctic Peninsula during the Cretaceous (Jefferson 1982a, 1983, Dettmann and Thomson 1987, Dettmann 1989, Cantrill 1995). The high representation of the conifer *Lagarostrobus*, which now prefers wet regions, in Late Cretaceous palynological assemblages and the rarity of *Classopollis* (Cheirolepidiaceae), tolerant of aridity (Francis 1984) and common elsewhere during the Cretaceous, is considered to reflect a steep latitudinal moisture gradient between South America and Antarctica (Askin and Spicer 1992). The interpretation of the Hidden Lake Formation and Santa Marta Formation fossil assemblages corroborates the relatively moist climatic conditions proposed for the southern high latitudes during the Late Cretaceous. Following this period, palaeobotanical evidence suggests humidity levels reduced and rainfall became more seasonal with a pronounced dry season (Askin 1992, Dutra 1998, Francis 1999).

From studies of the physiognomic characteristics of these Late Cretaceous leaf fossils, including the application of leaf margin analysis, SLR and MLR models, mean annual temperatures of 12-21°C were derived for the HLF flora and 14-23°C for the SMF flora. Both the Northern and Southern Hemisphere relationships between leaf margin and MAT proposed by Wolfe (1979) were used in the leaf margin analysis. The different relationship for the Southern Hemisphere takes into account the greater proportion of evergreen species in the Southern Hemisphere today. However, it is not clear whether evergreen or deciduous species were dominant in these high southern latitudes during the Cretaceous, when mild winter temperatures may have favoured the deciduous habit (Askin and Spicer 1992, Read and Francis 1992, Hill and Scriven 1995).

Published information on the palaeoclimate of the Antarctic Peninsula during the Late Cretaceous was reviewed in Chapter 1. Previously available palaeobotanical data suggested warming through the Cretaceous until the Maastrichtian when temperatures dropped. The results from this study compare well with published data on Late Cretaceous palaeoclimates. Applying leaf margin and leaf size analysis to an angiosperm flora of only six taxa, Rees and Smellie (1989) suggested mean annual temperatures of 13-20°C for the Cenomanian-Campanian of Livingston Island, South Shetland Islands. Francis (1999) compiled a graph of palaeotemperatures for the Antarctic Peninsula through the Late Cretaceous and Tertiary using evidence from fossil floras. The results from this study have been used to modify this curve (Figure 7.3). This new data from fossil leaf physiognomy indicates that the Coniacian-Santonian was a time of considerable warmth during the Late Cretaceous.
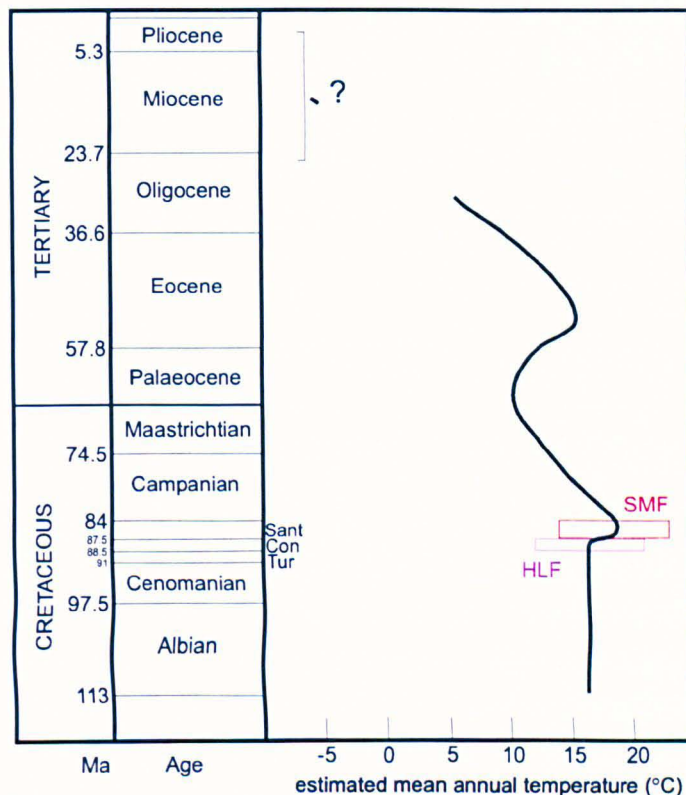
Figure 7.3 Estimated mean annual temperatures for the Antarctic Peninsula through the Late Cretaceous and Tertiary based on palaeobotanical data.

(Edited from Francis 1999 and updated with new results from this study).
HLF – Hidden Lake Formation flora, SMF – Santa Marta Formation flora.

Palaeoclimatic interpretations of sedimentary and marine isotope evidence have also been previously published for the Antarctic Peninsula. Dingle and Lavelle (1998) have made palaeoclimatic interpretations for the Late Cretaceous James Ross Island area derived from geochemical analysis of sedimentary rocks. Based on the assumption that the fossil floras of the Late Cretaceous of the Antarctic Peninsula signal high humidity, the degree of weathering of feldspars (CIA index) and sediment maturity was considered to reflect ambient temperatures. Strong chemical weathering during the Santonian-Campanian (Santa Marta Formation) suggested a period of peak warmth and humidity followed by falling temperatures towards the end of the Cretaceous (Figure 7.4).
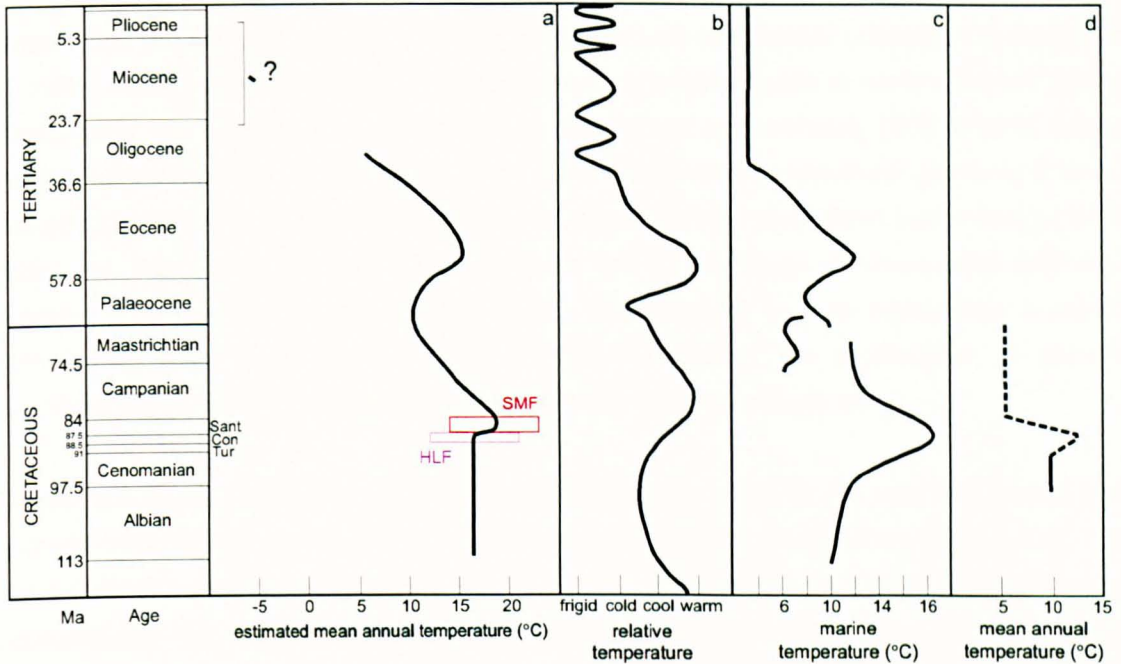
Figure 7.4 Estimated palaeotemperatures through the Late Cretaceous and Tertiary.

a. Estimated mean annual temperatures for the Antarctic Peninsula based on palaeobotanical data. (Edited from Francis 1999 and updated with new results from this study). HLF – Hidden Lake Formation flora, SMF – Santa Marta Formation flora.
b. Relative temperatures for the northern Antarctic Peninsula based on geochemical analyses. (Redrawn from Dingle and Lavelle 1998).
c. Marine temperatures for the northern Antarctic Peninsula based on $\delta^{18}O$ data in Ditchfield et al. (1994), Barrera et al. (1987), Pirrie et al. (1998), Zachos et al. (1993). (Redrawn from Dingle and Lavelle 1998).
d. Estimated mean annual temperatures for the North Slope of Alaska. (Redrawn from Parrish and Spicer 1988).

Late Cretaceous ocean temperatures have been estimated using oxygen isotopes from the James Ross Basin (Pirrie and Marshall 1990, Marshall et al. 1993, Ditchfield et al. 1994) (Figure 7.4). Analysis of oysters gives mean temperatures of 18.5°C for the Hidden Lake Formation and temperatures estimated for the Santa Marta Formation are 19.2°C using ammonites and 13.5°C using belemnites. Ditchfield et al. (1994) suggested that temperatures were relatively cool during the Aptian-Cenomanian, with peak warming during the Coniacian-Santonian and cooling later in the Cretaceous. This trend compares well with the palaeobotanical results, but there are difficulties in the interpretation of palaeotemperature trends from this isotope data. The cooler temperatures calculated for the Aptian-Coniacian may reflect the deposition of these strata in relatively deep marine settings, while the later Cretaceous formations were deposited in shallow marine environments. The temperatures predicted for the Hidden Lake Formation may also be anomalously high because these estimates were derived only from epifaunal oysters. These oysters may have inhabited $\delta^{18}O$ depleted bottom waters, which may have resulted in overestimation of palaeotemperatures. The inferred progressive fall in temperatures from a high in the Santonian-Campanian to the end of the Cretaceous is more reliable. These strata were all deposited in shallow marine environments and errors introduced by possible vertical isotopic stratification and vital effects were constrained by the analysis of various fossil groups from both epifaunal and nektonic habitats (Ditchfield et al. 1994).

Using palaeobotanical data, Wolfe and Upchurch (1987) modelled a lower latitudinal temperature gradient of 0.3°C per 1° of latitude for the Late Cretaceous (compared to 0.5°C per 1° today, Francis and Frakes 1993). These workers reported a period of relative warmth for the Santonian of North America, a mean annual temperature of approximately 25°C at 30°N. Based on this temperature at 30°N and the lower Late Cretaceous temperature gradient, a mean annual temperature of approximately 15°C is predicted for the James Ross Island area at 65°S during the Santonian. This falls within the lower end of the range of temperature estimates provided by these Antarctic fossil assemblages. Temperatures may be higher than expected from extrapolation using this latitudinal gradient because of the amelioration of climatic conditions through the maritime effect on the Antarctic Peninsula island arc.

Parrish and Spicer (1988) constructed a palaeotemperature curve for the Late Cretaceous high northern latitudes based on leaf margin analysis and vegetation physiognomy (Figure 7.4). This curve indicates peak warming during the Coniacian. Maximum mean annual temperatures of approximately 13°C for the North Slope of Alaska are lower than those estimated in this study for the Antarctic Peninsula during the Coniacian. However, during the Late Cretaceous the North Slope is believed to have been situated at 80-85°N. Based on the latitudinal temperature gradient modelled for the Late Cretaceous, maximum MATs of 17.5-19°C are predicted for latitudes of 65°S. These estimates fall within the range of temperatures derived from this study of leaf physiognomy for this Late Cretaceous period on the Antarctic Peninsula.

Direct comparison with the results of computer modelling of Cretaceous climates (e.g. by Barron et al. 1994) is not possible because the models are based on broad Cretaceous palaeogeography for an unspecified time within the Cretaceous. During the Cretaceous Antarctica was not isolated by cold circum-polar currents, the position of land masses allowed ocean currents to transport heat from low to high latitudes and the maritime effect on the Antarctic Peninsula may have allowed more uniform climates (Francis and Frakes 1993). The models predict that increased CO_2 levels would have raised global temperatures in a 'greenhouse' Earth.

In conclusion, available palaeoclimatic data from various sources implies that the Coniacian-early Campanian was a period of considerable warmth on the Antarctic Peninsula. The results from this study may support suggestions that this was the warmest time during the Late Cretaceous which was followed by climate cooling, a trend observed globally from many climate indicators.

8 Summary

This is the first study of these Late Cretaceous fossil angiosperm leaf assemblages and it provides new information on the Antarctic Peninsula flora composition and palaeoclimate. This final chapter summarises the main conclusions reached in this project.

Angiosperm leaf assemblages are preserved within Late Cretaceous strata of the James Ross Basin adjacent to the Antarctic Peninsula. These fossils represent the remains of vegetation that grew on an emergent volcanic arc situated about 65°S. The leaves were transported into the back arc basin by rivers that drained from the Antarctic Peninsula land area to the west and were preserved in the shallow marine sediments now exposed on James Ross Island. The Hidden Lake Formation flora (Coniacian) was preserved within a deltaic environment and the Santa Marta Formation flora (Santonian-early Campanian) within a mid- to outer-shelf setting.

The leaf fossils are isolated and fragmentary impressions or permineralisations, but although no cuticle is present, the leaf architecture is generally well preserved. Approximately 25% of the leaves of both floras are almost whole. Leaf bases are preserved in about 50% of the leaves and apices in approximately 25%. Although many leaves are represented by fragmentary material, leaf margins are present in at least 80% of the fossils and venation patterns are generally clear. Some of the leaves show evidence of pre-abscission damage, including wound reaction tissue, which may represent arthropod feeding, and possible galling resulting from insect interaction.

Angiosperm leaves dominate the floras comprising approximately 70% of the collections, with some ferns, and rare conifer and bennettitalean remains. However, the degree of fragmentation and small leaf size observed in these allochthonous assemblages is indicative of strong taphonomic biases that have impacted on this study of floral composition and palaeoclimate. The synchronous leaf abscission of deciduous dicotyledonous angiosperm trees and shrubs and sorting within the water column may have contributed to the abundance of angiosperm leaves and increased proportions of particular taxa. The best preserved leaves within these floras and the morphotypes established are probably representative of certain species that are most resistant to pre-abscission damage, fragmentation and decay. In an attempt to account for these processes, even the most fragmentary specimens were included in the study. The occurrence of these large leaf collections within marine sediments may reflect some catastrophic event, such as flooding and storms. Although this suggests that these floras may contain juvenile leaves assigned to separate taxa, it is expected that these fossil floras are an indication of minimum diversity on the Antarctic Peninsula. The fossil assemblages probably represent plants growing on the delta top and homogeneous streamside vegetation with a mixture of leaves from various sites along the rivers. The recognition of this bias may be supported by the identification of a high proportion of narrow leaf forms within these floras.

The degree of fragmentation of these fossil leaves caused difficulties in the isolation and identification of taxonomic groups, but the fine detail of leaf architecture was preserved allowing detailed study of features significant in dicotyledonous angiosperm leaf identification. These features include leaf form and apical and basal styles, the nature of the leaf margin, types of venation and the patterns displayed by the primary, secondary, tertiary and higher vein orders. The classification scheme set out by Hickey (1973, 1979) was useful in precise description of leaf outline and venation characteristics well preserved in these Late Cretaceous fossils and the popularity of this terminology facilitated comparison with previous studies of fossil and living angiosperm leaf forms.

In order to group these Cretaceous Antarctic leaves into distinct taxa or morphotypes based on shared architectural characteristics several approaches were undertaken. Initial attempts included visual assessment of observed morphology and an artificial classification based on only one character (venation type). Isolating groups visually was difficult because these Cretaceous leaves appeared to form a morphological continuum and the fragmentary nature of the leaves prohibited direct comparison of features between specimens. Single character classification was unsuccessful because there is not one single character preserved in all, or at least, most of the leaf fossils on which grouping could be initiated.

Multivariate statistical analysis allowed more than one leaf character to be used simultaneously in classification. Previously established methods used in the partitioning of angiosperm leaf taxa could not be used in this study because many of the required characters were not present in these Antarctic fossils (e.g. gland position, cuticular features, and measurements requiring whole leaf preservation). Recommendations from previous approaches were considered and a new method was constructed using 23 characters frequently preserved in angiosperm leaf impressions. These characters included features of lamina symmetry, form, apical and basal styles, margin type, presence of a petiole, venation type, primary vein size and course, secondary vein divergence angles and courses, presence of intersecondary veins or an intramarginal vein, and tertiary vein angles.

First attempts at scoring the characters in this study involved converting all characters so that they could be scored in a binary format. Although nine of the characters were successfully scored as binary or two-state characters (e.g. presence of an intramarginal vein or lamina symmetry), binary coding of many of the features preserved in these Cretaceous leaves was found to be statistically unacceptable. Nine qualitative multistate characters (e.g. apex form) were especially valuable in this study since although quantitative measurement of angles or lengths could not be used for incomplete leaves it was generally possible to assign features to categories. The remaining five characters concerning angles formed by secondary and tertiary veins were scored as quantitative continuous characters to impart greater discriminatory power to these frequently preserved features.

In order to quantify resemblance between these angiosperm leaves based on the combination of binary, multistate and continuous characters found to be most useful in this study, the General Similarity Coefficient of Gower was selected. Clustering analysis was then performed and dendrograms for the Hidden Lake Formation and Santa Marta Formation floras were produced. This clustering output was used in conjunction with the original leaf drawings and descriptions to group leaves of similar morphologies.

However, there is a high percentage of missing data in these fragmentary fossil leaf collections (51% in the Hidden Lake Formation flora, 41% in the Santa Marta Formation flora). A fairly large number of leaves clustered together because they were too fragmentary. The clustering analysis was therefore repeated with the most fragmentary specimens removed and morphotypes were delineated based on the best preserved leaves. The less well preserved leaves were then assigned to these morphotypes by repeated analyses using subsets of the characters available in the fragmentary specimens. Using this approach it was possible to assign even very fragmentary material to morphotypes and clearly establish where fragmentary leaves represented separate taxa.

Combined with knowledge of the leaf specimens from the original drawings and descriptions, this multivariate statistical approach was used to group these Late Cretaceous Antarctic angiosperm leaves and a total of 41 morphotypes were defined. Of these, 30 are present within the Hidden Lake Formation flora and 31 within the Santa Marta Formation flora, with 20 common to both floras.

Although statistical methods were implemented, the morphotypes established are considered equivalent to fossil form genera, which are also defined based on assessment of morphological characteristics. Using a statistical approach, however, allows many characters to be taken into account simultaneously and may allow more objective decisions on grouping. This type of coding allows a detailed account of the range of features observed in a fossil taxon to be stored in a concise format and may facilitate comparative studies with both fossil and living plants.

The distinguishing characteristics of each morphotype were described and illustrated and comparisons were drawn with fossil and living angiosperm leaves. The dominant leaf form in both the Hidden Lake Formation and Santa Marta Formation floras is considered to show similarity to the Magnoliales and both floras share a strong component of sterculiaceous- and lauralean-like leaf forms. A morphotype sharing diagnostic features with leaves of the Elaeocarpaceae is also common to both floras. There are rare leaf fossils showing similarities to the Atherospermataceae and Annonaceae within the Hidden Lake Formation flora. Morphotypes with architectural characteristics typical of the Cunoniaceae and Nothofagaceae occur within the Hidden Lake Formation flora but are more abundant within the Santa Marta Formation flora. Restricted to the slightly later Santa Marta Formation is a morphotype showing similarities to the Myrtaceae.

Most of these examples of angiosperm families possessing leaves showing similarities to the Late Cretaceous leaf morphotypes in this study have already been recognised on the Antarctic Peninsula. There is support for the assignment of the Coniacian-Santonian fossil leaves in this study to the Cunoniaceae, Myrtaceae, Lauraceae and possible Winteraceae from wood and pollen records of the same age. If the botanical affinities suggested by leaf architectural features can be confirmed, then these new leaf records would extend the ranges of some families (e.g. Atherospermataceae, Elaeocarpaceae, Nothofagaceae and Sterculiaceae) in Antarctica.

In the Late Cretaceous, there were still land connections between Antarctica and the other Gondwanan continents and the Antarctic Peninsula is believed to have provided an important migratory pathway during the evolution and diversification of the angiosperms in the Southern Hemisphere. The results from this study may offer support to the theories that certain plant groups, such as the Nothofagaceae, originated in West Antarctica. There may also be support for the idea that different groups of angiosperms migrated to Antarctica from two different directions during the Late Cretaceous.

The presence of leaf forms showing similarities to leaves of plants such as the Sterculiaceae, Lauraceae, Elaeocarpaceae, Atherospermataceae, Cunoniaceae and Myrtaceae are suggestive of warm and moist conditions on the Antarctic Peninsula during the Late Cretaceous. The leaves showing similarities to those of groups such as the Nothofagaceae and Winteraceae are, on the other hand, indicative of cooler temperatures. The possible coexistence of plants with apparently different thermal requirements may reflect mixing within streams of leaves from different altitudes and different local climates on the high relief volcanic arc. However, taphonomic bias and the uncertain identification of these Late Cretaceous morphotypes does not allow reliable palaeoclimate interpretation using this nearest living relative approach. In addition, the possibility that these floras represent successional vegetation growing in disturbed streamside environments during active volcanism may mean that leaf physiognomy is not in tune with environmental conditions.

Studies of leaf physiognomy, including analysis of leaf margins and sizes and the application of simple linear regression and multiple linear regression models provided estimates of temperatures and precipitation on the Antarctic Peninsula during the Late Cretaceous. Mean annual temperatures of 12-21°C for the Hidden Lake Formation flora and 14-23°C for the Santa Marta Formation flora were predicted. Using SLR and MLR models, precipitation estimates calculated were 54-272cm (MAP) and 215-311cm (GSP) for the Hidden Lake Formation flora and 59-257cm (MAP) and 197-293cm (GSP) for the Santa Marta Formation flora.

Precipitation predictions are highly tentative because these results are strongly affected by taphonomic factors. The tendency towards incomplete preservation of leaf apices means that MLR equations do not provide reliable precipitation estimates. Overrepresentation of streamside species may lead to overestimation of precipitation, but there are several taphonomic processes resulting in an underestimation of leaf size and a corresponding underestimation of

precipitation. These include catastrophic events leading to the preservation of juvenile foliage, a bias towards the accumulation of 'sun' leaves, and sorting and fragmentation within the water column. Attempts to reconstruct the original sizes of the fragmentary leaf specimens may have reduced the effects of some of these processes, but it is considered that the precipitation estimates derived from SLR models are minimum estimates of actual precipitation on the Antarctic Peninsula during the Late Cretaceous. Mean annual temperature estimates based on leaf margin characters are generally considered robust to taphonomic processes, so the estimates of temperatures on the Antarctic Peninsula during the Late Cretaceous are provided with some confidence.

The estimates of mean annual temperatures obtained in this study point to considerable warmth on the Antarctic Peninsula in the Coniacian-early Campanian. Comparisons with previously reported interpretations of the climate from other Antarctic fossil floras suggest warming through the Cretaceous until the onset of cooling in the Maastrichtian. A similar trend is observed in temperature records based on analysis of sedimentary geochemistry and marine oxygen isotopes in the James Ross Island area. A parallel drawn with palaeobotanical evidence for palaeotemperatures in the high northern latitudes suggests that the results from this study may reflect a period of peak global warmth.

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Appendix 1 - Terminology

A   Hickey classification for angiosperm leaves

The main features of Hickey's (1973) scheme are outlined below to aid in the understanding of terminology used in this thesis. Most diagrams are modified from Hickey (1973) and Hickey (1979).

A1. Leaf orientation:
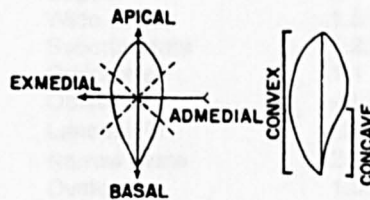
Figure A-1 Leaf architectural features – orientation.

A2. Leaf organisation:
Simple: consisting of a single lamina, all parts of which are connected by foliar tissue.
Compound: leaf divided into separate laminar sub-units.
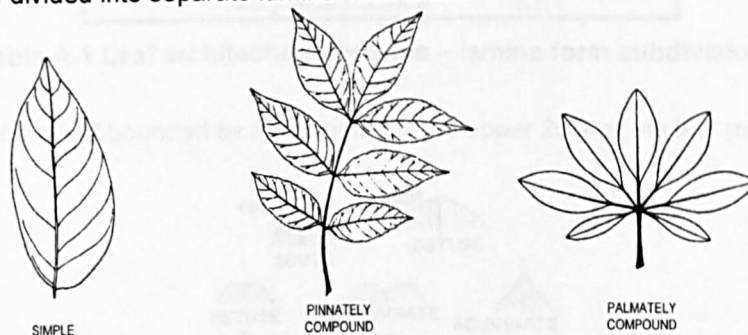
Figure A-2 Leaf architectural features – leaf organisation.

A3. Leaf shape:
Lamina:
Symmetry:
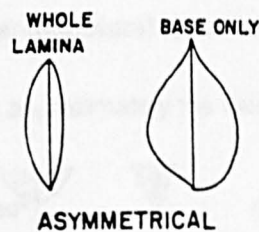
Figure A-3 Leaf architectural features – symmetry.

Form: These definitions were modified by Hickey from Stearn (1956). The four main types are shown in Figure A-4 and are defined by the point where the axis of greatest width intersects the long axis of the leaf. These types are further subdivided using the length-width (l/w) ratios in Table A-1. The ratios for the subclasses are lower limits except for the last.
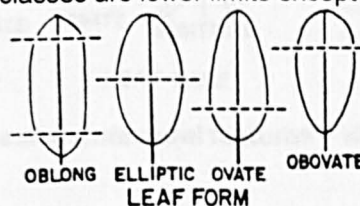
Figure A-4 Leaf architectural features – lamina form.

Form	Subdivision	l/w ratio
Oblong	Linear	≥10:1
	Lorate	6:1
	Narrow oblong	3:1
	Oblong	2:1
	Wide oblong	1.5:1
	Very wide oblong	≤1.2:1
Elliptic	Very narrow elliptic	≥6:1
	Narrow elliptic	3:1
	Elliptic	2:1
	Wide elliptic	1.5:1
	Suborbiculate	1.2:1
	Orbiculate	1:1
	Oblate	≤0.75:1
Ovate	Lanceolate	≥3:1
	Narrow ovate	2:1
	Ovate	1.5:1
	Wide ovate	1.2:1
	Very wide ovate	≤1:1
Obovate	Narrow oblanceolate	≥6:1
	Oblanceolate	3:1
	Narrow obovate	2:1
	Wide obovate	1.2:1
	Very wide obovate	≤1:1

Table A-1 Leaf architectural features – lamina form subdivisions.

Apex: portion of the leaf bounded by approximately the upper 25% of the leaf margin.
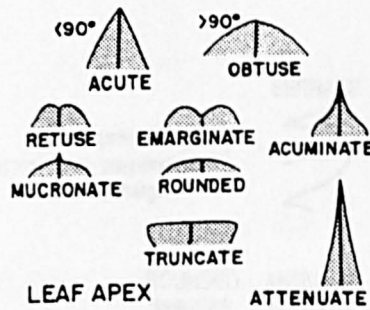
Figure A-5 Leaf architectural features – shape of apex.

Base: portion of the leaf bounded by approximately the lower 25% of the leaf margin.
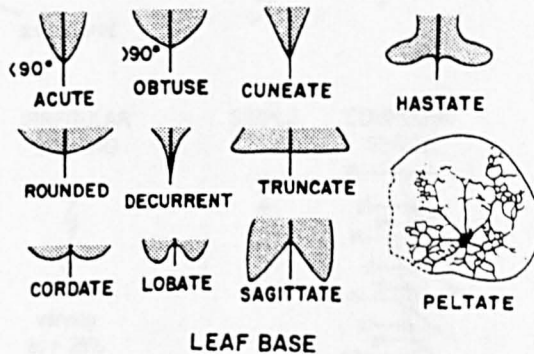
Figure A-6 Leaf architectural features – shape of base.

A4. Form of leaf margin:

ENTIRE — smooth

LOBED — indented >= 1/4 of distance to midvein or long axis of leaf

TOOTHED — projections with pointed apices, indented <1/4 of distance to midvein or long axis of leaf

CRENATE — smoothly rounded projections

EROSE — irregular

REVOLUTE — rolled up
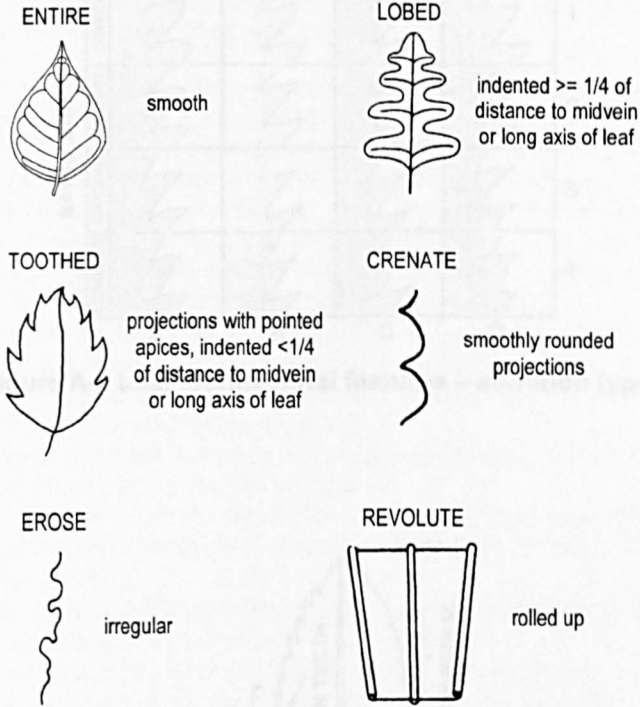
Figure A-7 Leaf architectural features – marginal features.

DENTATE — axes of symmetry approximately perpendicular to trend of margin

SERRATE — axes of symmetry at an oblique angle to trend of margin

PARTS OF A TOOTH

SINUS
APICAL SIDE
TOOTH APEX
BASAL SIDE

ROUNDED SINUSES

ANGULAR SINUSES

sinuses are the incisions between marginal projections of any sort

REGULAR SPACING — varying by < 25%

IRREGULAR SPACING — varying by > 25%

SIMPLE SERIES

COMPOUND SERIES

Figure A-8 Leaf architectural features – tooth features.
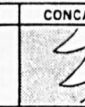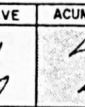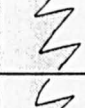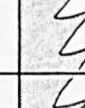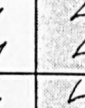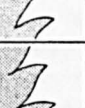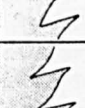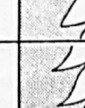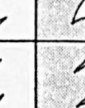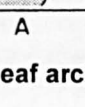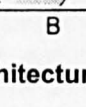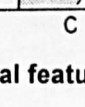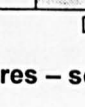
Figure A-9 Leaf architectural features – serration type.

A5. Gland position:
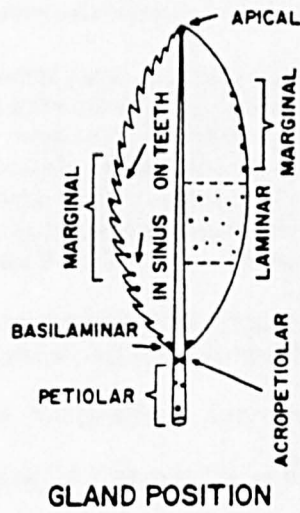
GLAND POSITION

Figure A-10 Leaf architectural features – gland position.

A6. Petiole:

Normal: without thickenings or other processes.
Inflated: thickened.
Winged: with a narrow strip of foliar tissue on each side.
Absent.

A7. Venation type:

Leaves with pinnate venation possess a single primary vein, while palmately veined leaves possess two or more equally prominent primary veins.

Pinnate: with a single primary vein (midvein) serving as the origin for the higher order venation.
    Craspedodromous: secondary veins terminating at the margin.
        Simple: all of the secondary veins and their branches terminating at the margin.
        Semicraspedodromous: secondary veins branching just within the margin, one of the branches terminating at the margin, the other joining the superadjacent secondary.
        Mixed: some of the secondary veins terminating at the margin and an approximately equal number of (usually intervening) secondaries otherwise.
    Camptodromous: secondary veins not terminating at the margin.
        Brochidodromous: secondaries joined together in a series of prominent arches.
        Eucamptodromous: secondaries upturned and gradually diminishing apically inside the margin, connected to the superadjacent secondaries by a series of cross veins without forming prominent marginal loops.
        Reticulodromous: secondaries losing their identity toward the leaf margin by repeated branching into a vein reticulum or network.
        Cladodromous: secondaries freely ramified or branching outward toward the margin.
    Hyphodromous: all but the primary vein absent, rudimentary, or concealed within a thick or fleshy mesophyll.
Parallelodromous: two or more primary veins originating beside each other at the leaf base and running parallel to the apex where they converge.
Campylodromous: several primary veins or their branches, originating at, or close to, a single point and running in strongly developed, recurved arches before converging toward the leaf apex. Vein pattern convergent above and below.
Acrodromous: two or more primary or strongly developed secondary veins running in convergent arches toward the leaf apex. Arches not recurved at base.
    a)   Position:
        Basal: acrodromous veins originating at the base of the leaf.
        Suprabasal: acrodromous veins originating some distance above the leaf base.
    b)   Development:
        Perfect: acrodromous veins well developed, running at least two-thirds of the distance to the leaf apex.
        Imperfect: acrodromous veins running less than two-thirds of the distance to the leaf apex.
Actinodromous: three or more primary veins diverging radially from a single point.
Palinactinodromous: primaries diverging in a series of dichotomous branchings, either closely or more distantly spaced.
The following categories apply to both the actinodromous and palinactinodromous vein categories.
    a)   Position of the first point of primary vein radiation:
        Basal: initial point of radiation at the leaf base.
        Suprabasal: initial point of radiation located some distance above the leaf base.
    b)   Development:
        Perfect: ramifications or branches of the lateral actinodromous veins covering at least two-thirds of the blade area.
        marginal: actinodromous veins reaching the margin.
        reticulate: actinodromous veins not reaching the margin.
        Imperfect: veins originating on the lateral actinodromous primary veins covering less than two-thirds of the blade area.
        marginal.
        reticulate.
        Flabellate: several to many equally fine basal veins diverge radially at low angles and branch apically.

TYPES OF VENATION

CRASPEDODROMOUS

HYPHODROMOUS | PARALLELO-DROMOUS

SEMICRASPEDODROMOUS | MIXED CRASPEDODROMOUS

CAMPTODROMOUS

SIMPLE CRASPEDODROMOUS

BROCHIDODROMOUS EUCAMPTODROMOUS RETICULODROMOUS CLADODROMOUS

ACTINODROMOUS

PERFECT

ACRODROMOUS

MARGINAL

RETICULATE

PERFECT

SUPRABASAL

BASAL

BASAL SUPRABASAL

BASAL SUPRABASAL

IMPERFECT

CAMPYLODROMOUS

IMPERFECT

MARGINAL RETICULATE

FLABELLATE

PALINACTINODROMOUS

BASAL SUPRABASAL

Figure A-11 Leaf architectural features – vein configuration.

A8. Orders of venation:

A8.1. Primary veins (1°):

Size: determined midway between the leaf apex and base as the ratio of vein width (vw) to leaf width (lw).

$$Size = vw/lw \times 100\%$$

Massive	>4%
Stout	2-4%
Moderate	1.25-2%
Weak	<1.25%

Course:
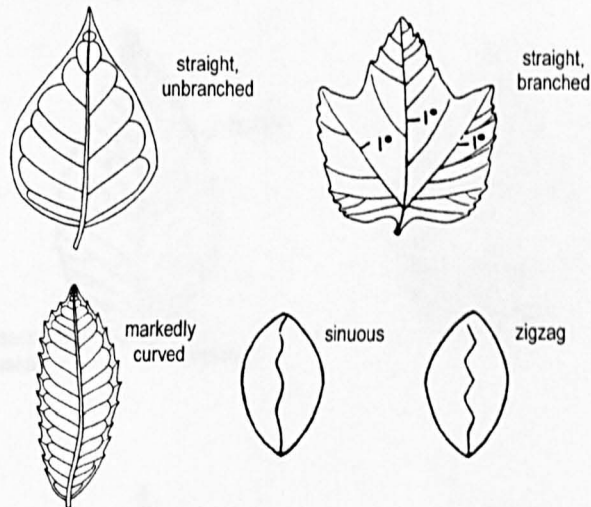
Figure A-12 Leaf architectural features – course of primary veins.

A8.2 Secondary veins (2°):

Angle of divergence: measured between the branch and the continuation of the source vein above the point of branching (Figure 13).
Acute: <80°: *Narrow*: <45°; *Moderate*: 45-65°; *Wide*: 65-80°.
Right-angle or approximately so: 80-100°.
Obtuse: >100°.

Variations in angle of divergence: nearly uniform divergence angle is the general case and departures from this are often taxonomically useful features.
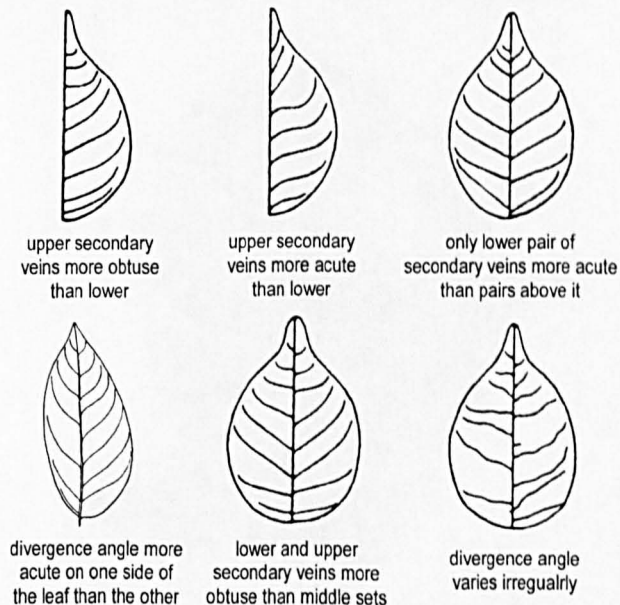
Figure A-13 Leaf architectural features – variation in secondary vein angle of divergence.

Relative thickness of secondary veins: a measure of the width of the secondary veins compared to the widths of the primary and tertiary orders. Such relative estimates of thickness for this and succeeding vein orders are a measure of the proportional reduction in width from one vein order to the next. This is a useful character only in cases of marked departure from the width expected in the proportional reduction series.

Thick: proportionally wide in relation to the primary and tertiary vein orders or to the secondaries in other leaves of similar size.

Moderate: the general case.

Fine to hair-like: proportionally narrow in relation to the primary and tertiary vein order or to the secondaries in other leaves of similar size.

Course: more than one term may apply.
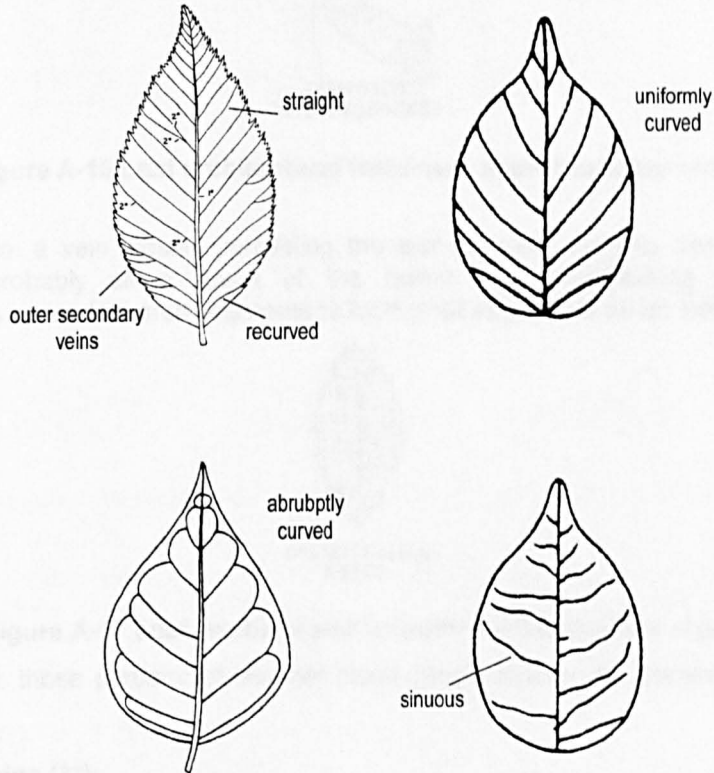
Figure A-14 Leaf architectural features – secondary vein course.
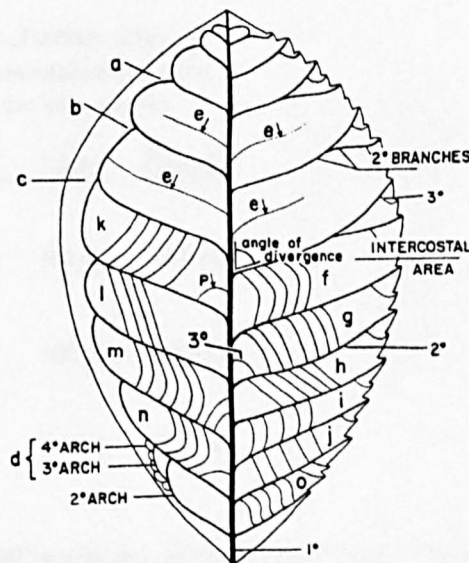
Figure A-15 Leaf architectural features – secondary and tertiary vein patterns.

Behaviour of loop-forming branches (if any):
Joining superadjacent secondary at an acute angle (Figure A-15 (a)).
Joining superadjacent secondary at a right-angle (Figure A-15 (b)).
Joining superadjacent secondary at an obtuse angle (Figure A-15 (c)).
Enclosed by secondary, tertiary or quaternary arches (Figure A-15 (d)).
Forming an intramarginal vein – see Figure A-17.

Intersecondary veins:
Simple: (e) in Figure A-15.
Compound: made up of coalesced tertiary vein segments for more than 50% of its length.

COMPOSITE
INTERSECONDARY

Figure A-16 Leaf architectural features – intersecondary veins.

Intramarginal vein: a vein closely paralleling the leaf margins and into which the secondary veins merge, probably as a result of the fusion and straightening of the exmedial brochidodromous secondary arch segments to form what appears to be an independent vein.

INTRAMARGINAL
VEINS
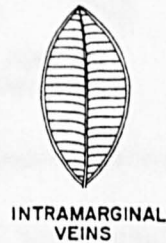
Figure A-17 Leaf architectural features – intramarginal veins.

Intercostal areas: those portions of the leaf blade lying between the secondary veins (Figure A-15).

A8.3. Tertiary veins (3°):

Angle of origin: terms used are the same as for the secondary veins and are defined above. When the average angle of tertiary origin on the exmedial (lower) side of the secondary veins is compared with the average on the admedial (upper) side of the secondary veins, the combinations shown in Table A-2 are possible.

			Angle of tertiary origin on the exmedial (lower) side of the secondaries		
			Acute	Right	Obtuse
Angle of tertiary origin on the admedial (upper) side of the secondaries		Acute	AA (f)	RA (l)	OA (l)
		Right	AR (g)	RR (j)	OR (m)
		Obtuse	AO (h)	RO (k)	OO (n)

Table A-2 Leaf architectural features – tertiary vein origin. The lower case letters in brackets refer to examples shown in Figure A-15.

As a rule, in tertiary veins originating on the admedial side of the secondary veins and curving to join the midvein, the angle of tertiary origin on the midvein equals the angle of tertiary origin on the exmedial side of the secondary veins of the leaf. Departure from this rule is a taxonomically significant feature.

Pattern: possible patterns of tertiary veins are illustrated in Figure A-15 and Figure A-18.
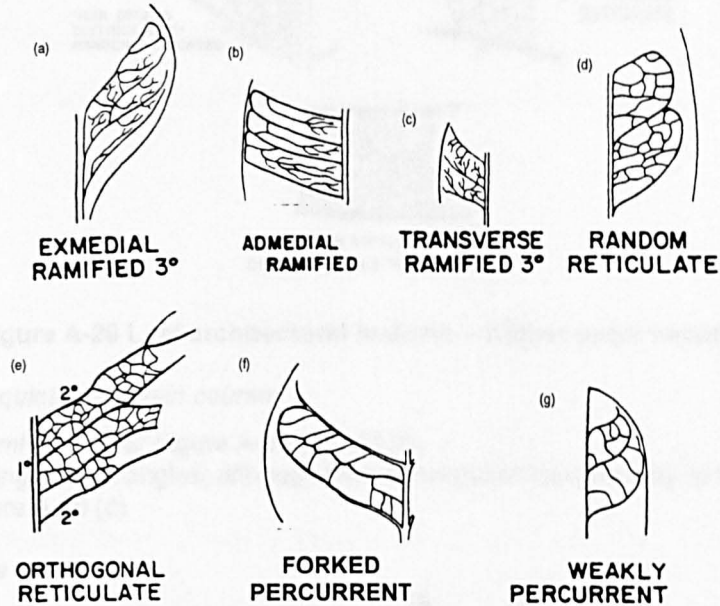
Figure A-18 Leaf architectural features – tertiary vein pattern.

Ramified: tertiary veins branching into higher orders without rejoining the secondary veins (although their higher order derivatives may do so). The categories of this type are shown in Figure A-18 (a), (b) and (c).
Reticulate: tertiary veins anastomosing with other tertiary veins or with the secondary veins. The categories of this type are shown in Figure A-18 (d) and (e).
Percurrent: tertiaries from the opposite secondaries joining.

> *Course of percurrent tertiary veins*:
>
> *Simple*: Figure A-15.   *Concave*: Figure A-15 (n).
> *Forked*: Figure A-18 (f).   *Sinuous*: Figure A-18 (g).
> *Straight*: Figure A-15 (h) and (l).   *Retroflexed*: Figure A-15 (o).
> *Convex*: Figure A-15 (f).   *Recurved*: Figure A-15 (p).

Relationship of percurrent tertiary veins to midvein:
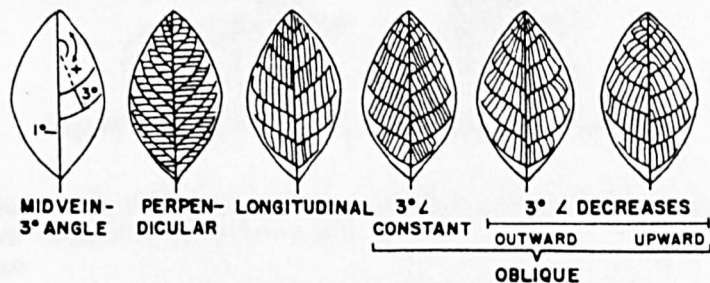
Figure A-19 Leaf architectural features – relationship of percurrent tertiary veins to midvein.

> *Arrangement of percurrent tertiary veins*:
> *Predominantly alternate*: Figure A-18 (f).
> *Predominantly opposite*: Figure A-15.
> *Alternate and opposite in about equal proportions*.
> *Distant*: <3 veins/cm.
> *Close*: >3 veins/cm.

A8.4. Higher order venation:
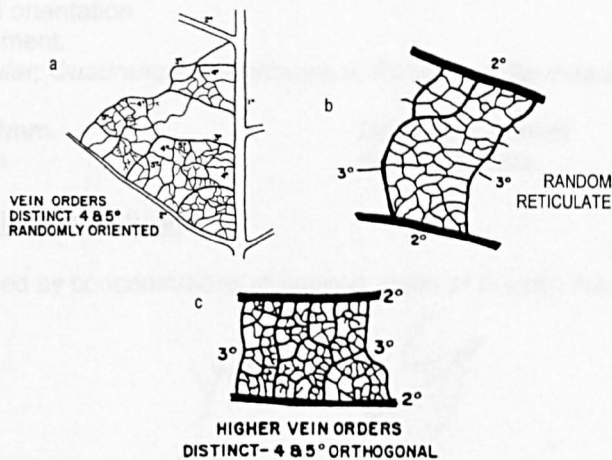
Figure A-20 Leaf architectural features – higher order venation.

Quaternary and quinternary vein course:

Relatively randomly oriented: Figure A-20 (a) and (b).
Orthogonal: arising at right angles, although their subsequent courses may or may not be at right angles Figure A-20 (c).

Marginal ultimate venation:
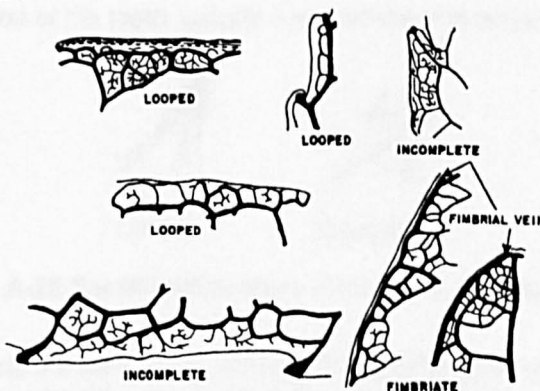
Figure A-21 Leaf architectural features – marginal ultimate venation.

Veinlets: freely ending ultimate veins of the leaf and veins of the same order which occasionally cross areoles to become connected distally.
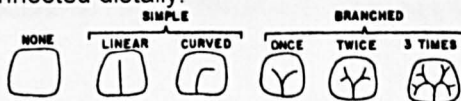
Figure A-22 Leaf architectural features – veinlets.

Areoles: the smallest areas of the leaf tissue surrounded by veins which taken together form a contiguous field over most of the area of the leaf.
Areole development:
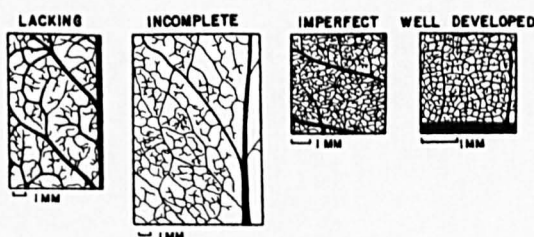
Figure A-23 Leaf architectural features – areole development.

Areole arrangement:
Random: no preferred orientation.
Oriented: similar alignment.
Areole shape: Triangular; Quadrangular; Pentagonal; Polygonal; Rounded; Irregular.
Areole size:

Very large: >2mm.	*Medium:* 1-0.3mm.
Large: 2-1mm.	*Small:* <0.3mm.

A9. Elements of tooth architecture:

Glandularity: recognised by concentrations of opaque material in tooth apex.

NON-GLANDULAR   **DARK GLANDULAR**
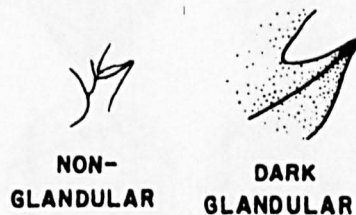
Figure A-24 Tooth architecture.

Apical termination of tooth:
Simple: tooth apex formed by the change in direction of the leaf margin without additional elements.
Papillate: clear, nipple shaped, glandular apical termination.

Principal vein configuration of the tooth: usually a secondary or a tertiary.
Course of vein:

CENTRAL   ECCENTRIC
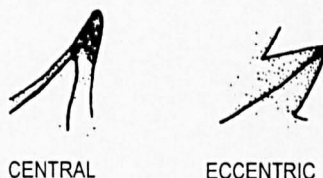
Figure A-25 Tooth architecture – course of principal vein.

Origin of vein:
Direct: running straight into the tooth as a continuation of the laminar venation.
Deflected: either arising just below the point of the marginal sinus, or the laminar vein which runs to the tooth branches equally before entering it, with one branch entering the tooth and the other running to the sinus.
Accessory veins:
Absent, incomplete or *looped.*
Present: joining with the principal vein or connivent with the principal vein.

B   Leaf rank categories (Hickey 1977)

LEAF RANK

Table A2-1 Preservation of the Hidden Lake Formation flora specimens.

Specimen Number	Leaf completeness	Missing portions of leaf	Preservation	Venation	Organic material	? Insect damage	Surface v. uneven	Margins	Apex present	Base present	Both apex and base	Petiole present
D8754.8.1a	almost whole	lower LHS	Excellent	Very clear	Medium, even	central holes		Clear	yes	incomplete	yes	no
D8754.8.2a	almost whole	centre and lower LHS	Excellent	Clear	Thin, even	-		Clear	yes	yes	yes	no
D8754.8.3a	almost whole	lower RHS	Excellent	Very clear	Medium, even	-		Clear	yes	yes	yes	no
D8754.8.2a&3a		3a shows best preservation										
D8754.8.4a	fragment	most of lower LHS, apex, base; lower RHS incomplete	Good	Very clear	Medium, even	-		Small %	incomplete	no	no	no
D8754.8.5a	fragment	most of lower RHS, apex, base; lower LHS incomplete	Fairly good	Fairly clear	Medium, even	-		Small %	incomplete	no	no	no
D8754.8.4a&5a		4a shows better preservation										
D8754.8.4b	fragment	apex, base, margins	Fairly good	Very clear	Medium, even	-		None	no	no	no	no
D8754.8.5b	fragment	apex, base, margins	Fair	Clear	Medium, even	-		None	no	no	no	no
D8754.8.4b&5b		4b shows better preservation										
D8754.8.4c	fragment	lower LHS; RHS incomplete	Very good	Very clear	Medium, even	-	yes	Small %	yes	incomplete	yes	no
D8754.8.4d	small fragment	LHS, upper RHS	Fairly good	Fairly clear	Thick, patchy	-		Clear	no	incomplete	no	no
D8754.8.5d	small fragment	apex; central parts and lower LHS incomplete	Fairly poor	Unclear	Thick, patchy	-		Small %	no	incomplete	no	yes
D8754.8.6a	small fragment	apex, base, margin unclear; central parts incomplete	Fair	Clear	Thin, even	-		Small %	no	no	no	no
D8754.8.6b	fragment	apex, base; RHS incomplete	Fairly good	Clear	Impression, thin	-		Clear	no	no	no	no
D8754.8.65a	fragment	apex, base; central parts incomplete	Fairly good	Clear	Medium, patchy	-		Clear	no	no	no	no
D8754.8.6b&65a												
D8754.8.7a	small fragment	apex, LHS; lower RHS incomplete	Fairly good	Clear	Medium, uneven	-		Clear	no	incomplete	no	no
D8754.8.8a	almost whole	apex incomplete	Excellent	Very clear	Thick, patchy	central holes		Clear	incomplete	incomplete	yes	no
D8754.8.9a	almost whole		Good	Fairly clear	Thick, patchy	central holes		Clear	yes	yes	yes	no
D8754.8.8a&9a		8a shows better preservation										
D8754.8.8b	small fragment	RHS, upper LHS	Fairly good	Fairly clear	Thick	-		Clear	no	incomplete	no	no
D8754.8.11b	small fragment	apex, base; RHS incomplete	Fair	Fairly clear	Medium, even	-		Clear	no	no	no	no
D8754.8.14b	small fragment	apex, base, RHS, margins; LHS incomplete	Fair	Clear	Thin, uneven	-		None	no	no	no	no
D8754.8.15a	small fragment	apex, base; central parts incomplete	Fair	Clear	Medium, uneven	-		Small %	no	no	no	no
D8754.8.16a	small fragment	apex; central parts and lower LHS incomplete	Fairly good	Clear	Thick, patchy	-		Small %	no	incomplete	no	yes
D8754.8.16b	fragment	apex; RHS and base incomplete	Good	Clear	Thick, patchy	-		Clear	no	incomplete	no	yes
D8754.8.16e	small fragment	apex, base, margins; central parts incomplete	Fairly poor	Fairly clear	Medium, uneven	-		None	no	no	no	no
D8754.8.16f	small fragment	apex, base, margins; central parts incomplete	Fairly poor	Fairly clear	Medium, uneven	-		None	no	no	no	no
D8754.8.17b	small fragment	apex, base; central parts incomplete	Poor	Unclear	Medium, uneven	-		Small %	no	no	no	no
D8754.8.17c	small fragment	apex, base, margins; central parts incomplete	Very poor	Unclear	Medium, uneven	-		None	no	no	no	no
D8754.8.21a	fragment	apex, base; central parts incomplete	Fairly good	Clear	Dark venation	-		Clear	no	no	no	no
D8754.8.46e	fragment	apex, base; central parts incomplete	Fairly good	Fairly clear	Dark venation	-		Clear	no	no	no	no
D8754.8.21a&46e												
D8754.8.22a	small fragment	apex; central parts incomplete	Fairly poor	Unclear	Thick, patchy	-		Small %	no	incomplete	no	no
D8754.8.22b	small fragment	apex, base; central parts incomplete	Fair	Fairly clear	Medium-thin	-	yes	Clear	no	no	no	no
D8754.8.24b	small fragment	apex, base, margins; central parts incomplete	Fairly poor	Fairly clear	Medium	-		None	no	no	no	no
D8754.8.25a	small fragment	base and central parts; apex incomplete	Fair	Fairly unclear	Thick, patchy	-		Small %	incomplete	no	no	no
D8754.8.26a	small fragment	apex, base, margins; central parts incomplete	Fairly poor	Fairly clear	Thin, patchy	-		None	no	no	no	no
D8754.8.26c	small fragment	apex, LHS; lower RHS incomplete	Fair	Fairly clear	Thin, patchy	-		Small %	no	incomplete	no	no
D8754.8.27a	small fragment	LHS, base; upper RHS incomplete	Fairly good	Very clear	Medium, even	-		Small %	incomplete	no	no	no
D8754.8.28a	almost whole	upper LHS; apex and margins incomplete	Good	Fairly clear	Thin, patchy	-		Clear	no	incomplete	no	no
D8754.8.30a	almost whole	apex; base and margins incomplete	Good	Clear	Medium, uneven	-	yes	Clear	no	incomplete	no	no

Table A2-1 Preservation of the Hidden Lake Formation flora specimens.

Specimen Number	Leaf completeness	Missing portions of leaf	Preservation	Venation	Organic material	? Insect damage	Surface v. uneven	Margins	Apex present	Base present	Both apex and base	Petiole present
D8754.8.31a	fragment	apex, base; central parts incomplete	Fairly good	Clear	Thin, uneven	-		Clear	no	no	no	no
D8754.8.32a	small fragment	apex, base, LHS; RHS incomplete	Fair	Fairly clear	Medium, patchy	-		Clear	no	no	no	no
D8754.8.98e	small fragment	apex, base, LHS; RHS incomplete	Fair	Fairly clear	Medium, patchy	-		Clear	no	no	no	no
D8754.8.32a&98e												
D8754.8.33a	small fragment	apex; central parts and base incomplete	Fairly good	Clear	Variable	-		Clear	no	incomplete	no	yes
D8754.8.34a	fragment	apex, base; margins incomplete	Fairly good	Fairly clear	Thin, patchy	-		Clear	no	no	no	no
D8754.8.34b	small fragment	base; central parts and apex incomplete	Fairly good	Fairly clear	Medium, patchy	-		Clear	incomplete	no	no	no
D8754.8.35a	almost whole	apex; central parts incomplete	Good	Fairly clear	Thick, patchy	-		Clear	no	incomplete	no	yes
D8754.8.37a	fragment	apex and base	Fairly good	Fairly clear	Thin	-		Clear	no	no	no	no
D8754.8.35a&37a												
D8754.8.36a	almost whole	apex; central parts incomplete	Good	Fairly clear	Medium, even	-		Clear	no	yes	no	yes
D8754.8.38a	fragment	apex and base; central parts incomplete	Fairly good	Clear	Medium	-		Small %	no	no	no	no
D8754.8.38b	small fragment	apex and base; margins and central parts incomplete	Poor	Unclear	Medium	-		Small %	no	no	no	no
D8754.8.39a	almost whole	tiny percentage of margins incomplete	Excellent	Clear	Thick-medium	-		Clear	yes	yes	yes	no
D8754.8.39b	small fragment	apex and base; central parts incomplete	Poor	Unclear	Thick	-		Small %	no	no	no	no
D8754.8.40a	fragment	apex; margins incomplete	Good	Fairly clear	Thick, uneven	-		Clear	no	yes	no	yes
D8754.8.41a	almost whole	very tip of leaf and basal margins incomplete	Excellent	Very clear	Medium, even	-		Clear	incomplete	incomplete	yes	no
D8754.8.42a	fragment	apex; margins, central parts and base incomplete	Good	Very clear	Thin, even	-		Clear	no	incomplete	no	no
D8754.8.43a	almost whole	apex; margins incomplete	Very good	Very clear	Thin, even	reaction tissue		Clear	no	incomplete	no	no
D8754.8.44a	fragment	apex; basal margins incomplete	Good	Clear	Thick, even	-		Clear	no	incomplete	no	no
D8754.8.44b	small fragment	apex and base; margins and central parts incomplete	Fairly good	Clear	Medium, patchy	-		Clear	no	no	no	no
D8754.8.45a	almost whole	upper RHS incomplete	Excellent	Very clear	Medium, even	-		Clear	incomplete	incomplete	yes	yes
D8754.8.45b	small fragment	apex, base, LHS; RHS incomplete	Fair	Fairly clear	Thick, uneven	-		Clear	no	no	no	no
D8754.8.46a	fragment	apex; central parts and base incomplete	Good	Clear	Thick-medium	-		Clear	no	incomplete	no	yes
D8754.8.46d	almost whole	apical and basal margins incomplete	Good	Clear	Medium, even	-		Clear	incomplete	no	no	no
D8754.8.47a	fragment	most of LHS; margins of RHS incomplete	Fairly good	Fairly clear	Medium, uneven	-		Clear	incomplete	no	no	no
D8754.8.47b	small fragment	apex, base and margins; central parts incomplete	Fairly poor	Fairly clear	Medium, patchy	-		None	no	no	no	no
D8754.8.47c	small fragment	apex, base and LHS; RHS incomplete	Fairly poor	Fairly unclear	Medium, patchy	-		Small %	no	no	no	no
D8754.8.48a	fragment	apex, base; margins and central parts incomplete	Fairly good	Very clear	Thick, uneven	-		Small %	no	no	no	no
D8754.8.48b	small fragment	apex, base, margins and RHS; central LHS incomplete	Fair	Clear	Medium, uneven	-		None	no	no	no	no
D8754.8.49a	almost whole	apex and lower LHS	Fairly good	Fairly unclear	Thick, uneven	-		Clear	no	incomplete	no	yes
D8754.8.49b	small fragment	apex and LHS; base and RHS incomplete	Fair	Fairly unclear	Thick, patchy	-		Clear	no	incomplete	no	no
D8754.8.49c	small fragment	LHS; apex and base of RHS incomplete	Fairly poor	Fairly unclear	Medium, patchy	-		Small %	no	no	no	no
D8754.8.50a	fragment	margins; central parts incomplete	Fair	Fairly unclear	Medium, uneven	-		None	incomplete	incomplete	no	yes
D8754.8.50b	small fragment	LHS and base; RHS incomplete	Fair	Fairly unclear	Medium, patchy	-		Small %	incomplete	no	no	no
D8754.8.54a	almost whole	apex and margins incomplete	Excellent	Very clear	Thin, even	central holes		Clear	incomplete	incomplete	yes	no
D8754.8.54b	small fragment	LHS and apex; margins and base incomplete	Fair	Fairly unclear	Thin, patchy	-		Clear	no	incomplete	no	no
D8754.8.56a	almost whole	margins, apex and base incomplete	Very good	Clear	Dark venation	-		Clear	incomplete	incomplete	yes	no
D8754.8.56b	small fragment	apex, base and margins; central parts incomplete	Fairly poor	Fairly unclear	Medium, patchy	-		Small %	no	no	no	no
D8754.8.57a	almost whole	apex and margins incomplete	Excellent	Very clear	Medium, holey	-		Clear	incomplete	yes	yes	no
D8754.8.58a	small fragment	RHS and upper LHS; central parts incomplete	Fairly good	Fairly clear	Thick, patchy	-		Clear	no	incomplete	no	no
D8754.8.58b	small fragment	apex, base and margins; central parts incomplete	Fair	Clear	Dark venation	-		None	no	no	no	no
D8754.8.59a	small fragment	base and central parts; apex incomplete	Fair	Fairly unclear	Thick, holey	-		Clear	incomplete	no	no	no

Specimen Number	Leaf completeness	Missing portions of leaf	Preservation	Venation	Organic material	? Insect damage	Surface v. uneven	Margins	Apex present	Base present	Both apex and base	Petiole present
D8754.8.59c	small fragment	apex, base and margins; central parts incomplete	Fair	Clear	Medium, even	reaction tissue		None	no	no	no	no
D8754.8.60a	fragment	apex and RHS, central parts incomplete	Good	Very clear	Medium, even	reaction tissue		Clear	no	incomplete	no	no
D8754.8.60b	small fragment	apex and base; central parts incomplete	Poor	Unclear	Thin, patchy	-		Small %	no	no	no	no
D8754.8.61a	fragment	apex and margins; base and central parts incomplete	Fairly good	Fairly clear	Dark venation	-		Small %	no	incomplete	no	no
D8754.8.62a	fragment	apex and base; central parts incomplete	Fairly good	Clear	Thick, uneven	-		Clear	no	no	no	no
D8754.8.64a	fragment	apex; central parts incomplete	Good	Fairly clear	Medium, uneven	-	yes	Clear	no	yes	no	no
D8754.8.62a&64a												
D8754.8.63a	almost whole	margins incomplete	Very good	Fairly clear	Variable	-		Clear	yes	incomplete	yes	no
D8754.8.66b	small fragment	apex and base; central parts and margins incomplete	Fairly poor	Fairly unclear	Thin, patchy	-		Small %	no	no	no	no
D8754.8.67a	small fragment	apex, base, margins and LHS; central parts incomplete	Fair	Very clear	Dark venation	-		None	no	no	no	no
D8754.8.67b	almost whole	apex; central parts and base incomplete	Good	Clear	Thick, patchy	-		Clear	no	incomplete	no	no
D8754.8.68a	fragment	apex; margins and base incomplete	Good	Clear	Variable	-		Clear	no	incomplete	no	no
D8754.8.68b	small fragment	apex, base, margins, LHS; RHS incomplete	Fairly good	Very clear	Medium, patchy	-		Small %	no	no	no	no
D8754.8.71b	small fragment	apex, base, margins, most of central parts	Fair	Clear	Dark venation	-		None	no	no	no	no
D8754.8.71c	small fragment	apex, base, margins, most of central parts	Very poor	Unclear	Medium	-		None	no	no	no	no
D8754.8.73b	small fragment	apex; central parts and base incomplete	Fair	Fairly clear	Medium	-		Small %	no	incomplete	no	yes
D8754.8.76b	small fragment	apex; central parts incomplete	Fairly good	Fairly unclear	Thick, uneven	-		Clear	no	yes	no	yes
D8754.8.81b	small fragment	apex, base, margins, most of central parts	Poor	Fairly unclear	Thick, patchy	-		None	no	no	no	no
D8754.8.82b	small fragment	apex, base, and most of central parts	Fair	Fairly clear	Medium, uneven	-		Small %	no	no	no	no
D8754.8.90b	small fragment	apex, base, margins; central parts incomplete	Poor	Fairly unclear	Dark venation	-		None	no	no	no	no
D8754.8.98a	almost whole	small piece of RHS; apex and base incomplete	Excellent	Very clear	Medium, even	-	yes	Clear	incomplete	incomplete	yes	no
D8754.8.98b	small fragment	apex, base, RHS; central LHS incomplete	Fair	Clear	Dark venation	-		Small %	no	no	no	no
D8754.8.98c	fragment	apex, base and central parts incomplete	Good	Clear	Medium, uneven	-		Small %	incomplete	incomplete	yes	no
D8754.8.98d	small fragment	apex; central parts and base incomplete	Fairly poor	Unclear	Thick, holey	-		Small %	no	incomplete	no	yes
D8754.8.100a	fragment	apex; central parts and base incomplete	Fairly good	Fairly clear	Thick, patchy	-		Clear	no	incomplete	no	no
D8754.8.101a	small fragment	apex, base, LHS; RHS incomplete	Fairly good	Very clear	Thin, uneven	-		Clear	no	no	no	no

Table A2-2 Preservation of the Santa Marta Formation flora specimens.

Specimen Number	Leaf completeness	Missing portions of leaf	Preservation	Venation	Organic material	? Insect damage	Surface v. uneven	Margins	Apex present	Base present	Both apex and base	Petiole present
D8604.37Aa	fragment	apex, base	good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8604.37A/Ca	fragment	apex, base	good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8604.37Ba	fragment	apex, base	good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8604.37A/Ca&Ba	fragment	apex, base	good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8604.38Aa	fragment	base; central parts incomplete	good	clear	carbonaceous impression	-		clear	yes	no	no	no
D8604.38Ba	fragment	base; central parts incomplete	very good	very clear	carbonaceous impression	-		clear	yes	no	no	no
D8604.38Aa&Ba	fragment	base; central parts incomplete	very good	very clear	carbonaceous impression	-		clear	yes	no	no	no
D8604.39a	fragment	apex; RHS of base incomplete	good	very clear	carbonaceous impression	-		clear	no	incomplete	no	no
D8604.54a	fragment	base; central parts incomplete	very good	very clear	cream mineralisation	-		clear	yes	no	no	no
D8605.1Aa	fragment	LHS, apex; base incomplete	fairly good	fairly clear	dark carbonaceous impression, charcoal, pyrite	-		clear	no	no	no	no
D8605.1Ba	fragment	RHS, apex; base incomplete	fairly good	fairly clear	dark carbonaceous impression	-		clear	no	no	no	no
D8605.1A&Ba	fragment	one side, apex; base incomplete	fairly good	fairly clear	dark carbonaceous impression	-		clear	no	no	no	no
D8605.2a	fragment	RHS, apex; central parts incomplete	good	very clear	carbonaceous impression	-		clear	no	incomplete	no	no
D8605.5a	fragment	apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		small %	no	no	no	no
D8605.15a	fragment	apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		small %	no	no	no	no
D8605a&15a	fragment	apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		small %	no	no	no	no
D8605.7a	small fragment	RHS, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8605.8Aa	small fragment	RHS, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8605.8Ba	small fragment	LHS, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8605.8Aa&8Ba	small fragment	one side, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8605.14a	small fragment	RHS, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		small %	no	no	no	no
D8605.16a	small fragment	RHS, apex, base; central parts incomplete	fair	fairly clear	carbonaceous impression	-		clear	no	no	no	no
D8605.19Aa	fragment	apex, central parts incomplete	good	clear	carbonaceous impression	-		clear	no	yes	no	yes
D8605.20a	small fragment	LHS, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8605.21Aa	fragment	apex; central parts and base incomplete	good	clear	dark carbonaceous impression	-		clear	no	incomplete	no	no
D8605.21Ba	fragment	apex; central parts and base incomplete	good	clear	dark carbonaceous impression	-		clear	no	incomplete	no	no
D8605.21Aa&21Ba	fragment	apex; central parts and base incomplete	good	clear	dark carbonaceous impression	-		clear	no	incomplete	no	no
D8605.22Ba	small fragment	apex, base, central parts incomplete	fair	clear	carbonaceous impression	-		small %	no	no	no	no
D8605.24a	small fragment	RHS, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8605.26a	small fragment	apex, base, margins; central parts incomplete	fair	very clear	carbonaceous impression, pyritised	-	yes	none	no	no	no	no
D8605.27Aa	small fragment	LHS, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8605.27Ba	small fragment	RHS, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8605.27Aa&Ba	small fragment	one side, apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		clear	no	no	no	no
D8605.28a	small fragment	apex, base, margins; central parts incomplete	fair	clear	carbonaceous impression	-		small %	no	no	no	no
D8605.29a	small fragment	apex, base, margins; central parts incomplete	fair	very clear	carbonaceous impression	-		none	no	no	no	no
D8605.30a	fragment	base; apex and central parts incomplete	good	clear	carbonaceous impression	-		clear	incomplete	no	no	no
D8605.31a	fragment	apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-		small %	no	no	no	no
D8605.33a	fragment	apex; central parts incomplete	very good	very clear	carbonaceous impression	-		clear	no	yes	no	no
D8606.4Aa	fragment	apex, base, RHS margin; central parts incomplete	fairly good	clear	carbonaceous impression	? mining		clear	no	no	no	no
D8606.4Ba	fragment	apex, base, LHS margin; central parts incomplete	fairly good	clear	carbonaceous impression	-		small %	no	no	no	no
D8606.4Aa&Ba	fragment	apex, base, margin on one side; central parts incomplete	fairly good	clear	carbonaceous impression	-		clear	no	no	no	no
D8606.5a	fragment	apex, central parts incomplete	good	fairly clear	carbonaceous impression	-		clear	no	yes	no	yes
D8606.6a	fragment	apex, base, most of margin; central parts incomplete	fair	fairly clear	carbonaceous impression	-		small %	no	no	no	no

Table A2-2 Preservation of the Santa Marta Formation flora specimens.

Specimen Number	Leaf completeness	Missing portions of leaf	Preservation	Venation	Organic material	? Insect damage	Surface v. uneven	Margins	Apex present	Base present	Both apex and base	Petiole present
D8606.7Aa	almost whole	base, LHS margin; apex incomplete	good	clear	carbonaceous impression	-		clear	incomplete	no	no	no
D8606.7Ba	almost whole	base, RHS margin; apex incomplete	good	clear	carbonaceous impression	-		clear	incomplete	no	no	no
D8606.7Aa&Ba	almost whole	base, margin on one side; apex incomplete	good	clear	carbonaceous impression	-		clear	incomplete	no	no	no
D8606.8a	fragment	apex, base, margins; central parts incomplete	fair	fairly clear	impression	-		none	no	no	no	no
D8609.147a	fragment	apex, base; central parts incomplete	fairly good	clear	carbonaceous impression	-	yes	clear	no	no	no	
D8610.1Aa	fragment	apex, base; central parts incomplete	good	very clear	carbonaceous impression	-		clear	no	no	no	
D8610.1Ba	fragment	apex, base; central parts incomplete	good	very clear	carbonaceous impression	-	yes	clear	no	no	no	
D8610.1Aa&Ba	fragment	apex, base; central parts incomplete	good	very clear	carbonaceous impression	-		clear	no	no	no	
D8616.74a	almost whole	margin unclear	good	fairly clear	impression	-		small %	incomplete	incomplete	yes	
D8616.128a	fragment	base; margin unclear, apex and central parts incomplete	fairly good	clear	impression, some mineralisation	-	yes	small %	incomplete	no	no	
D8618.106a	almost whole	apex, LHS margin	very good	very clear	impression, some mineralisation	-	yes	clear	no	yes	no	yes
D8619.6a	almost whole	apex, margin and central parts incomplete	good	clear	impression	-	yes	small %	no	incomplete	no	
D8619.7a	fragment	apex, base; central parts incomplete	good	very clear	carbonaceous impression	-	yes	clear	no	no	no	
D8619.12a	fragment	apex; central parts incomplete	very good	very clear	impression, some mineralisation	-	yes	clear	no	yes	no	
D8619.18a	almost whole	base and central parts incomplete	excellent	very clear	part carbonaceous impression, part mineralisation	-		clear	yes	incomplete	yes	
D8621.27a	fragment	apex, base; RHS margin and central parts incomplete	good	very clear	impression	-		clear	no	no	no	
D8625.119a	fragment	apex; base and central parts incomplete	good	very clear	impression	-		clear	no	incomplete	no	
DJ134.2Aa	fragment	central parts and base	good	clear	carbonaceous impression	-		clear	yes	no	no	
DJ134.2Ba	fragment	central parts and base	good	fairly clear	carbonaceous impression	-		clear	yes	no	no	
DJ134.2Aa&Ba	fragment	central parts and base	good	clear	carbonaceous impression	-		clear	yes	no	no	
DJ134.6a	fragment	apex and central parts	fair	fairly clear	carbonaceous impression	-	yes	clear	no	yes	no	
DJ134.11a	small fragment	apex, base, margin; central parts incomplete	fairly poor	fairly clear	carbonaceous impression	-	yes	none	no	no	no	
DJ134.12Aa	small fragment	apex, base, margin; central parts incomplete	fair	clear	carbonaceous impression	-		none	no	no	no	
DJ134.12Ba	small fragment	apex, base, margin; central parts incomplete	fair	clear	impression	-		none	no	no	no	
DJ134.12A&Ba	small fragment	apex, base, margin; central parts incomplete	fair	clear	carbonaceous impression	-		none	no	no	no	
DJ134.13a	almost whole	base; margin and central parts incomplete	fairly good	fairly clear	impression	-		small %	incomplete	no	no	
DJ134.15Aa	almost whole	central parts incomplete	excellent	fairly clear	carbonaceous impression	-		clear	yes	yes	yes	
DJ134.15Ba	almost whole	central parts incomplete	excellent	fairly clear	carbonaceous impression	-		clear	yes	yes	yes	
DJ134.15Aa&Ba	almost whole	central parts incomplete	excellent	fairly clear	carbonaceous impression	-		clear	yes	yes	yes	
DJ134.16a	fragment	apex; central parts incomplete	good	clear	impression, some mineralisation	-		clear	no	yes	no	yes
DJ134.21A/Ba	fragment	apex, margin; central parts and base incomplete	fairly good	clear	impression, some mineralisation	-		small %	no	incomplete	no	yes
DJ134.22A/Ba	almost whole	apex, base, margin and central parts incomplete	fairly good	fairly clear	impression	-	yes	small %	no	incomplete	no	
DJ134.27Ba	fragment	apex; central parts and base incomplete	fairly good	fairly clear	impression	-	yes	small %	no	incomplete	no	
DJ134.28Aa	fragment	RHS, apex, base; margin and central parts incomplete	fairly good	fairly clear	carbonaceous impression	-	yes	small %	incomplete	incomplete	no	
DJ147.1a	small fragment	central parts and base	fairly good	fairly unclear	mineralisation	-	yes	clear	yes	no	no	
DJ147.3a	small fragment	apex, base, margin and central parts incomplete	fair	very clear	carbonaceous impression	-		none	no	no	no	
DJ147.4a	fragment	apex, RHS; central parts and base incomplete	fairly good	very clear	impression, some mineralisation	-		clear	no	incomplete	no	
DJ147.6a	almost whole	apex and LHS incomplete	very good	very clear	carbonaceous impression	-	yes	clear	no	incomplete	no	
DJ147.7a	fragment	LHS, apex, base, margin; central parts incomplete	fair	clear	mineralisation	-		none	no	no	no	
DJ147.8a	fragment	RHS, apex, base; central parts incomplete	fairly good	clear	mineralisation, primary charcoalified	-		clear	no	no	no	
DJ147.9a	fragment	base; central parts incomplete	fairly good	clear	impression	-		clear	yes	no	no	
DJ147.15a	fragment	base; central parts incomplete	fairly good	clear	impression, some mineralisation	-		clear	yes	no	no	
DJ147.9a&15a	fragment	base; central parts incomplete	fairly good	clear	impression, some mineralisation	-		clear	yes	no	no	

Table A2-2 Preservation of the Santa Marta Formation flora specimens.

Specimen Number	Leaf completeness	Missing portions of leaf	Preservation	Venation	Organic material	? Insect damage	Surface v. uneven	Margins	Apex present	Base present	Both apex and base	Petiole present
DJ147.10a	almost whole	apex and central LHS incomplete	excellent	clear	carbonaceous impression, mineralisation	-	yes	clear	incomplete	yes	yes	no
DJ147.11a	almost whole	apex, base and central parts incomplete	excellent	very clear	mineralisation	-	yes	clear	incomplete	incomplete	yes	no
DJ147.12Aa	almost whole	base incomplete	excellent	clear	impression, mineralisation	-		clear	yes	incomplete	yes	no
DJ147.12Ba	almost whole	base incomplete	excellent	clear	impression, mineralisation	-		clear	yes	incomplete	yes	no
DJ147.12Aa&Ba	almost whole	base incomplete	excellent	clear	impression, mineralisation	-		clear	yes	incomplete	yes	no
DJ147.13a	small fragment	apex, base, margin; central parts incomplete	fair	very clear	impression, mineralisation	-		none	no	no	no	no
DJ147.14a	almost whole	apex, base and RHS incomplete	good	clear	carbonaceous impression	-	yes	clear	incomplete	no	no	no
DJ147.17a	fragment	apex, base; central parts incomplete	fairly good	clear	impression, mineralisation	-		small %	no	no	no	no
DJ147.18a	small fragment	RHS, apex, base; central parts incomplete	fair	clear	impression, mineralisation	-		small %	no	no	no	no
DJ147.19a	fragment	apex, LHS; central parts incomplete	good	very clear	impression, mineralisation	-		clear	no	incomplete	no	no
DJ147.54a	fragment	RHS, apex; central parts incomplete	good	very clear	impression, some mineralisation	-		clear	no	incomplete	no	no
DJ147.19a&54a	fragment	one side, apex; central parts incomplete	good	very clear	impression, mineralisation	-		clear	no	incomplete	no	no
DJ147.20a	fragment	central parts incomplete	good	clear	impression, mineralisation	-	yes	clear	no	incomplete	no	no
DJ147.23a	fragment	apex, base; central parts incomplete	fairly good	very clear	carbonaceous impression	-	yes	small %	no	no	no	no
DJ147.24a	fragment	apex, base; central parts incomplete	fairly good	clear	impression, mineralisation	-		clear	no	no	no	no
DJ147.25a	fragment	apex; base and central parts incomplete	good	clear	impression, mineralisation	reaction tissue	yes	clear	no	incomplete	no	no
DJ147.26a	small fragment	RHS, apex, base; central parts incomplete	fair	clear	impression, mineralisation	-		small %	no	no	no	no
DJ147.28a	small fragment	apex, base; central parts incomplete	fair	fairly clear	impression, mineralisation	-		small %	no	no	no	no
DJ147.29a	small fragment	apex, base; central parts incomplete	fair	clear	carbonaceous impression	-		small %	no	no	no	no
DJ147.30a	fragment	apex, base, RHS; central parts incomplete	fairly good	clear	carbonaceous impression	-	yes	clear	no	no	no	no
DJ147.31a	fragment	apex, base, LHS; central parts incomplete	fairly good	clear	impression, mineralisation	-	yes	clear	no	no	no	no
DJ147.32a	almost whole	apex, basal RHS and central parts incomplete	excellent	very clear	impression, mineralisation	-	yes	clear	incomplete	incomplete	yes	no
DJ147.33a	fragment	LHS, apex; central parts incomplete	fairly good	fairly clear	impression, mineralisation	-		clear	no	incomplete	no	no
DJ147.34a	small fragment	apex, base; central parts incomplete	fairly good	clear	impression, some mineralisation	-	yes	clear	no	no	no	no
DJ147.35a	fragment	apex, base; central parts incomplete	fairly good	fairly clear	impression, mineralisation	-		clear	no	no	no	no
DJ147.37Aa	almost whole	base and basal RHS incomplete	very good	clear	impression	-	yes	clear	yes	no	no	no
DJ147.37B/Ca	almost whole	base and LHS incomplete	excellent	clear	impression	-	yes	clear	yes	incomplete	yes	no
DJ147.37A&B/Ca	almost whole	base and one side incomplete	excellent	clear	impression	-	yes	clear	yes	incomplete	yes	no
DJ147.38Aa	fragment	LHS; apex, base and central parts incomplete	good	very clear	impression, mineralisation	-	yes	clear	no	incomplete	no	no
DJ147.39a	almost whole	basal RHS	excellent	very clear	impression, mineralisation	-	yes	clear	yes	incomplete	yes	yes
DJ147.40a	fragment	LHS, apex, base; central parts incomplete	fairly good	clear	impression, mineralisation	-	yes	clear	no	no	no	no
DJ147.41Aa	fragment	RHS; apex, base and central parts incomplete	fairly good	clear	impression, mineralisation	-	yes	clear	no	no	no	no
DJ147.43a	fragment	apex, base, margin; central parts incomplete	fairly good	clear	impression, mineralisation	-		small %	no	no	no	no
DJ147.44a	fragment	RHS, base and central parts incomplete	very good	fairly clear	impression, mineralisation	-	yes	clear	yes	incomplete	yes	yes
DJ147.45a	fragment	apex, base; central parts incomplete	fairly good	clear	impression, mineralisation	-	yes	clear	no	no	no	no
DJ147.46a	almost whole	apex and basal LHS incomplete, obscured by Ca	very good	clear	carbonaceous impression	-	yes	clear	incomplete	incomplete	yes	no
DJ147.48a	fragment	apex, LHS margin; central parts incomplete	fairly good	fairly clear	impression, mineralisation	? galls		clear	no	incomplete	no	yes
DJ147.49Aa	fragment	apex; central parts and base incomplete	good	very clear	impression, mineralisation	? galls	yes	clear	no	incomplete	no	no
DJ147.49Ba	fragment	apex; central parts and base incomplete	good	very clear	carbonaceous impression, mineralisation	? galls	yes	clear	no	no	no	no
DJ147.49A&Ba	fragment	apex; central parts and base incomplete	good	very clear	carbonaceous impression, mineralisation	? galls	yes	clear	no	incomplete	no	no
DJ147.51a	fragment	apex, base, margin and central parts incomplete	fairly good	clear	impression, mineralisation	-		small %	no	no	no	no
DJ147.52a	fragment	RHS, apex; central parts incomplete	good	clear	impression, mineralisation	-		clear	no	incomplete	no	no

Specimen Number	Leaf completeness	Missing portions of leaf	Preservation	Venation	Organic material	? Insect damage	Surface v. uneven	Margins	Apex present	Base present	Both apex and base	Petiole present
DJ147.53a	fragment	apex, base and central parts incomplete	good	clear	impression, mineralisation	-	yes	clear	no	incomplete	no	no
DJ147.55Aa	fragment	apex, base; central parts incomplete	good	very clear	carbonaceous impression	-		clear	no	no	no	no
DJ147.55Ba	fragment	apex, base; central parts incomplete	good	very clear	carbonaceous impression	-		clear	no	no	no	no
DJ147.55A&Ba	fragment	apex, base; central parts incomplete	good	very clear	carbonaceous impression	-		clear	no	no	no	no
DJ147.56a	fragment	LHS, apex; central parts incomplete	good	very clear	carbonaceous impression	-	yes	clear	no	incomplete	no	no
DJ147.59a	fragment	apex, base; margin and central parts incomplete	fairly good	fairly clear	impression, mineralisation	-		small %	no	incomplete	no	no
DJ147.60a	fragment	RHS, central parts and base	fairly good	fairly clear	impression, mineralisation	-		clear	incomplete	no	no	no
DJ147.60b	fragment	apex, base, LHS margin; central parts incomplete	fairly good	fairly clear	impression, mineralisation	-		clear	no	no	no	no
DJ451.7a	fragment	apex, base, margin; central parts incomplete	fairly good	clear	impression, mineralisation	-		small %	no	no	no	no
DJ452.2a	fragment	apex; central parts and base incomplete	good	clear	carbonaceous impression, mineralisation	-		clear	no	yes	no	yes

Table A2-2 Preservation of the Santa Marta Formation flora specimens.

Table A2-3 Hidden Lake Formation leaf measurements.

Specimen Number	Maximum length (mm)	Max. length est. (mm)	Maximum width (mm)	Max. width one half (mm)	Max. width est. (mm)	Area (sq. mm)	Area est. (sq. mm)	Max. length along primary (mm)	Max. length along primary est. (mm)	Leaf area (sq. mm)	Petiole length (mm)
D8754.8.1a	45.2		19.5	11.4 (RHS)	22.8	519.6 min.	683.9	43.2		687	-
D8754.8.2a	46.2		23.5			423.3 min.	528.4	46.4		726.9	-
D8754.8.3a	47.4		24.1			504.8 min.	556.8	47.6		764.8	-
D8754.8.2a&3a	46.8		23.8			464.1 min.	542.6	47		745.9	-
D8754.8.4a	48.7 min.	49.7 min.	18 min.	13.4 min. (RHS)	26.8 min.	518.3 min.	903.4 min.	47.7 min.	50 min.	893.3 min.	-
D8754.8.5a	48 min.	49.1 min.	19.8 min.	13 min. (LHS)	26 min.	511.8 min.	893.4 min.	46.8 min.	49.3 min.	851.1 min.	-
D8754.8.4a&5a	48.4 min.	49.4 min.	18.9 min.		26.4 min.	515.1 min.	898.4 min.	47.3 min.	49.7 min.	798.5 min.	-
D8754.8.4b	31.4 min.	34.3 min.	26.4 min.	13.8 min. (RHS)	27.6 min.	376.6 min.	752.8 min.	17.1 min.	34.3 min.	631.1 min.	-
D8754.8.5b	32 min.	33.4 min.	23.8 min.	12.4 min. (LHS)	24.8 min.	352 min.	702.2 min.	17 min.	33.4 min.	552.2 min.	-
D8754.8.4b&5b	31.7 min.	33.9 min.	25.1 min.		26.2 min.	364.3 min.	727.5 min.	17.1 min.	33.9 min.	591.7 min.	-
D8754.8.4c	43.1		21.9 min.	13.8 min. (RHS)	27.6 min.	404.1 min.	690.8 min.	40.7 min.	43.1	793 min.	-
D8754.8.4d	31.4 min.		22.6 min.	20.1 min. (RHS)	40.2 min.	425.4 min.	859.4 min.	21.3 min.	31.4 min.	841.5 min.	-
D8754.8.5d	42 min.	42.2 min.	13.4 min.	8.2 min. (LHS)	16.4 min.	235.1 min.	390 min.	41.6 min.	42.2 min.	461.4 min.	-
D8754.8.6a	18.4 min.	19.2 min.	14.3 min.	8.6 min. (LHS)	17.2 min.	109.9 min.	247 min.	13.3 min.	19.2 min.	220.2 min.	-
D8754.8.6b	46 min.	44.7 min.	33.9 min.	19.4 (LHS)	38.8	958.5 min.	1510.4 min.	33.4 min.	42.7 min.	1104.5 min.	-
D8754.8.65a	45.2 min.	51.6 min.	35.8 min.	20.4 (RHS)	40.8	876.2 min.	1749.2 min.	36.9 min.	51.9 min.	1411.7 min.	-
D8754.8.6b&65a	46 min.	51.6 min.	35.8 min.		39.8	958.5 min.	1749.2 min.	36.9 min.	51.9 min.	1377.1 min.	-
D8754.8.7a	32.2 min.	33.5 min.	10.3 min.	10.3 min.	20.6 min.	204.7 min.	480 min.	16.3 min.	33.5 min.	460.1 min.	-
D8754.8.8a	30		18.1			369.1 min.	369.9	30.1		363.2	-
D8754.8.9a	28.7		17.2			341.7		28.7		329.1	-
D8754.8.8a&9a	29.4		17.7			355.4 min.	355.8	29.4		346.2	-
D8754.8.8b	24.9 min.		12.7 min.	12.7 min. (LHS)	25.4 min.	191.9 min.	383.8 min.	16.2 min.	24.9 min.	421.6 min.	-
D8754.8.11b	7.8 min.		5.1 min.			22.2 min.		7 min.	7.8 min.	26.5 min.	-
D8754.8.14b	17.9 min.		10.1 min.	10.1 min. (LHS)	20.2 min.	88.5 min.	245.8 min.			241.1 min.	-
D8754.8.15a	25.6 min.	27.1 min.	21.8 min.	17.4 min. (RHS)	34.8 min.	320.4 min.	705.8 min.	24 min.	27.2 min.	631 min.	-
D8754.8.16a	27.1 min.	27.4 min.	17.8 min.	12.8 min. (RHS)	25.6 min.	249 min.	452.8 min.	25.6 min.	25.9 min.	442 min.	1.6
D8754.8.16b	16 min.		13.5 min.	7.7 (LHS)	15.4	129.7 min.	167.2 min.	12.7 min.		130.4 min.	3.2
D8754.8.16e	14.3 min.		9.4 min.	7.4 min. (LHS)	14.8 min.	72 min.	129.8 min.	13 min.	14.3 min.	141.1 min.	-
D8754.8.16f	26.9 min.		19.3 min.	19.3 min. (RHS)	38.6 min.	331.6 min.	663.2 min.			692.2 min.	-
D8754.8.17b	39.1 min.	40.3 min.	35.1 min.	20.7 min. (LHS)	41.4 min.	779.1 min.	1234.2 min.	32.9 min.	40.6 min.	1120.6 min.	-
D8754.8.17c	29.4 min.		15.6 min.	15.6 min. (RHS)	31.2 min.	272.3 min.	544.6 min.			611.5 min.	-
D8754.8.21a	14.5 min.	15.9 min.	11.3 min.	6.4 min. (LHS)	12.8 min.	104.8 min.	168.2 min.	11.8 min.	15.9 min.	135.7 min.	-
D8754.8.46e	14.7 min.	17.4 min.	11.1 min.	5.9 min. (RHS)	11.8 min.	118.1 min.	177.2 min.	13.1 min.	17.4 min.	136.9 min.	-
D8754.8.21a&46e	14.6 min.	16.7 min.	11.2 min.		12.3 min.	111.5 min.	172.7 min.	12.5 min.	16.7 min.	136.3 min.	-
D8754.8.22a	26.4 min.		18.3 min.			269 min.		27.4 min.		334.3 min.	-
D8754.8.22b	10.9 min.		13.2 min.			96.4 min.	122.6 min.	10.1 min.	10.9 min.	95.9 min.	-
D8754.8.24b	14.4 min.		13.4 min.			89.5 min.				128.6 min.	-
D8754.8.25a	12.1 min.		8.6 min.			61.9 min.	66.6 min.	11.5 min.	11.9 min.	68.2 min.	-
D8754.8.26a	14.2 min.	16.7 min.	16.7 min.	10.9 min. (LHS)	21.8 min.	154.2 min.	270.4 min.	7.2 min.	16.8 min.	244.2 min.	-
D8754.8.26c	16.1 min.		7.3 min.	6.6 min. (RHS)	13.2 min.	60.7 min.	113.4 min.	14.9 min.	16.1 min.	141.7 min.	-
D8754.8.27a	29.1 min.		11.8 min.	10 min. (RHS)	20 min.	155.9 min.	384.6 min.	29 min.		386.7 min.	-
D8754.8.28a	33.2 min.	34.1 min.	17.1			249.6 min.	363.4 min.	28.6 min.	33.9 min.	386.5 min.	-

Table A2-3 Hidden Lake Formation leaf measurements.

Specimen Number	Maximum length (mm)	Max. length est. (mm)	Maximum width (mm)	Max. width one half (mm)	Max. width est. (mm)	Area (sq. mm)	Area est. (sq. mm)	Max. length along primary (mm)	Max. length along primary est. (mm)	Leaf area (sq. mm)	Petiole length (mm)
D8754.8.30a	20.5 min.		16.4 min.	8.4 min. (LHS)	16.8 min.	237.5 min.	269.2 min.	18.9 min.	20.5 min.	229.6 min.	-
D8754.8.31a	23.8 min.	28.3 min.	16.9 min.	9.6 min. (LHS)	19.2 min.	223.3 min.	432.6 min.	12.3 min.	28.3 min.	362.2 min.	-
D8754.8.32a	18.4 min.		33.8 min.	33.8 min. (LHS)	67.6 min.	366.7 min.		9.2 min.	22.2 min.	1000.5 min.	-
D8754.8.98e	16.6 min.		32.1 min.	32.1 min. (RHS)	64.2 min.	334.8 min.		9.2 min.	20.7 min.	886 min.	-
D8754.8.32a&98e	17.5 min.		33 min.		66 min.	350.8 min.		9.2 min.	21.5 min.	946 min.	-
D8754.8.33a	34.5 min.	27.7 min.	21.3 min.	11.1 min. (LHS)	22.2 min.	271.7 min.	355.8 min.	22.2 min.	27.7 min.	410 min.	8.1
D8754.8.34a	32.9 min.	34.7 min.	16.5			384.7 min.	451.6 min.	26.4 min.	34.8 min.	382.8 min.	-
D8754.8.34b	16.8 min.		9.3 min.	6.1 min. (RHS)	12.2 min.	81.3 min.	115.2 min.	12.9 min.	16.8 min.	136.6 min.	-
D8754.8.35a	41.9 min.	37.8 min.	26.6			658.5 min.	715.5 min.	25.2 min.	37.8 min.	670.3 min.	4.6
D8754.8.37a	34.3 min.	38.3 min.	26.7			573.1 min.	718.6 min.	20.2 min.	38.3 min.	681.7 min.	-
D8754.8.35a&37a	41.9 min.	38.1 min.	26.7			658.5 min.	717.1 min.	25.2 min.	38.1 min.	676 min.	4.6 (35a)
D8754.8.36a	28.9 min.	27.4 min.	17.3			313.7 min.	353.7 min.	25.3 min.	27.6 min.	318.3 min.	1.9
D8754.8.38a	27.7 min.	33.5 min.	18.5			340.6 min.	475.4 min.	26.3 min.	33.5 min.	413.2 min.	-
D8754.8.38b	5.4 min.		11.6 min.	9.3 min. (RHS)	18.6 min.	39 min.	68.8 min.	2.6 min.	5.4 min.	67 min.	-
D8754.8.39a	21.8		8.2			128.5		21.8		119.2	-
D8754.8.39b	13.9 min.	15.2 min.	9.4 min.	9.4 min. (LHS)	18.8 min.	89.1 min.	202 min.	5.3 min.	15.2 min.	190.5 min.	-
D8754.8.40a	22.7 min.	23.2 min.	16.4			256.6 min.	283.8 min.	21.3 min.	23.3 min.	254.7 min.	0.5
D8754.8.41a	48.4 min.		18.6			592.2 min.		48.6 min.		602.6 min.	-
D8754.8.42a	35.5 min.	38 min.	21.1			548.2 min.	650 min.	35 min.	38 min.	534.5 min.	-
D8754.8.43a	32.5 min.	32.9 min.	16			373.4 min.	388.1 min.	31.2 min.	33 min.	352 min.	-
D8754.8.44a	58.2 min.	60.3 min.	21.6			814.2 min.	871 min.	57.5 min.	60.3 min.	868.3 min.	-
D8754.8.44b	8.7 min.		4.4 min.	3 min. (RHS)	6 min.	19.8 min.	28.8 min.	8.1 min.	8.7 min.	34.8 min.	-
D8754.8.45a	41.7	38.4	18.9 min.	10.1 min. (LHS)	20.2	419.6 min.	504.2	38.5		518.5	3.3
D8754.8.45b	29.2 min.		19.1 min.			300.2 min.		-	29.2 min.	371.8 min.	-
D8754.8.46a	20.5 min.	21.4 min.	14.2 min.	8.3 min. (LHS)	16.6	152.8 min.	245 min.	14.2 min.	21.5 min.	237.9 min.	1
D8754.8.46d	12.2 min.	12.3 min.	5.8 min.			48.3 min.	51.5 min.	11.3 min.	11.8 min.	47.6 min.	-
D8754.8.47a	33 min.		12.1 min.	8.6 min. (RHS)	17.2 min.	183.4 min.	289.2 min.	28 min.	33 min.	378.4 min.	-
D8754.8.47b	20.3 min.	20.5 min.	16.8 min.	10.1 min. (RHS)	20.2 min.	181.7 min.	303.6 min.	20.1 min.	20.5 min.	276.1 min.	-
D8754.8.47c	19.1 min.	20.4 min.	14 min.	14 min. (RHS)	28 min.	166.3 min.	484.8 min.	10.4 min.	20.2 min.	377.1 min.	-
D8754.8.48a	53.4 min.	54.5 min.	13.5 min.	10 min. (RHS)	20 min.	439.4 min.	822.6 min.	50.4 min.	54.5 min.	726.7 min.	-
D8754.8.48b	22.9 min.		22.3 min.	22.3 min. (LHS)	44.6 min.	291.5 min.	583 min.	-	-	680.9 min.	-
D8754.8.49a	71.5 min.	65.8 min.	16.1			564 min.	772.6 min.	65.3 min.	66.4 min.	712.7 min.	7.9
D8754.8.49b	31.1 min.		19.7 min.	19.7 min. (RHS)	39.4 min.	309.5 min.	619 min.	22.1 min.	31.1 min.	816.9 min.	-
D8754.8.49c	25.4 min.		10.5 min.	10.5 min. (RHS)	21 min.	176.2 min.	352.4 min.	20.3 min.	25.4 min.	355.6 min.	-
D8754.8.50a	50.8 min.	38 min.	24.2 min.	12.6 min. (RHS)	25.2 min.	460.6 min.	649.4 min.	32.1 min.	38.1 min.	640.1 min.	15.8
D8754.8.50b	26.1 min.		15.3 min.	12.4 min. (RHS)	24.8 min.	208.7 min.	463.4 min.	26.7 min.		441.4 min.	-
D8754.8.54a	59.5 min.	59.8 min.	20.5			738.4 min.	842.8 min.	58.8 min.	60 min.	820 min.	-
D8754.8.54b	33.9 min.		13.6 min.	10.7 min. (RHS)	21.4 min.	285.7 min.	571.4 min.	27.8 min.	33.9 min.	483.6 min.	-
D8754.8.56a	35.2 min.		13.7 min.			268.7 min.	317.6 min.	-		321.5 min.	-
D8754.8.56b	18.1 min.	19.5 min.	16.4 min.	8.9 min. (RHS)	17.8 min.	162.6 min.	315.4 min.	12.9 min.	19.6 min.	232.6 min.	-
D8754.8.57a	37.3 min.		10.6			249.8 min.	264.4 min.	36.9 min.	37.3 min.	263.6 min.	-
D8754.8.58a	65.9 min.	67.2 min.	45.4 min.	45.4 min. (LHS)	90.8 min.	1608.7 min.	4925.8 min.	-	-	4067.8 min.	-

Table A2-3 Hidden Lake Formation leaf measurements.

Specimen Number	Maximum length (mm)	Max. length est. (mm)	Maximum width (mm)	Max. width one half (mm)	Max. width est. (mm)	Area (sq. mm)	Area est. (sq. mm)	Max. length along primary (mm)	Max. length along primary est. (mm)	Leaf area (sq. mm)	Petiole length (mm)
D8754.8.58b	7.7 min.	8.4 min.	17.8 min.	11.6 min. (RHS)	23.2 min.	43.6 min.	154.4 min.	5 min.	8.4 min.	129.9 min.	-
D8754.8.59a	11 min.	11.7 min.	8.9 min.	5.3 min. (LHS)	10.6 min.	51.5 min.	65.4 min.	11 min.	11.8 min.	83.4 min.	-
D8754.8.59c	31.7 min.	33.3 min.	16 min.	8.3 min. (LHS)	16.6 min.	169.6 min.	500.8 min.	25.6 min.	33.3 min.	368.5 min.	-
D8754.8.60a	53 min.	53.3 min.	28.1 min.	23 min. (LHS)	46 min.	753.2 min.	1893 min.	45.5 min.	53.3 min.	1634.5 min.	-
D8754.8.60b	15.3 min.		11.1 min.			126.6 min.		13.8 min.	15.3 min.	113.2 min.	-
D8754.8.61a	41.7 min.	42.4 min.	35.4 min.	25.5 min. (LHS)	51 min.	758.5 min.	1309.4 min.	40 min.	42.4 min.	1441.6 min.	-
D8754.8.62a	33.5 min.	36 min.	32.7 min.		39.3 min.	594.1 min.	926.3 min.	23.9 min.	37.1 min.	972 min.	-
D8754.8.64a	33.5 min.	36 min.	25.4 min.		39.3 min.	505.8 min.	926.3 min.	24.5 min.	37.1 min.	972 min.	-
D8754.8.62a&64a	34.7 min.	36 min.	39.3 min.			788.5 min.	926.3 min.	28 min.	37.1 min.	972 min.	-
D8754.8.63a	51.7		26.3 min.			744.2 min.	802.3 min.	52		911.7 min.	-
D8754.8.66b	42.4 min.	46.4 min.	24.3			521.6 min.	822.4 min.	26.4 min.	46.4 min.	751.7 min.	-
D8754.8.67a	38.7 min.	42 min.	13.6 min.	13.1 min. (RHS)	26.2 min.	303.2 min.	791.6 min.	23.5 min.	42.1 min.	735.3 min.	-
D8754.8.67b	15.9 min.		9.7 min.	6.2 (LHS)	12.4	107.5 min.	154.2 min.	12.8 min.	15.9 min.	131.4 min.	-
D8754.8.68a	21.7 min.	23.7 min.	15.3 min.	7.7 min. (RHS)	15.4 min.	167.7 min.	224.4 min.	20.6 min.	23.8 min.	244.3 min.	-
D8754.8.68b	23 min.		19.6 min.	19.6 min. (RHS)	39.2 min.	251.6 min.	503.2 min.	-	-	601.1 min.	-
D8754.8.71b	6.8 min.		4.9 min.			19.7 min.		-	-	22.2 min.	-
D8754.8.71c	12.9 min.		16.5 min.			127.4 min.		-	-	141.9 min.	-
D8754.8.73b	11.3 min.		13.9 min.	13.5 min. (LHS)	27 min.	50.4 min.	164.4 min.	5.6 min.	11.3 min.	203.4 min.	-
D8754.8.76b	33.4 min.	25.5 min.	9.1 min.	6.1 min. (RHS)	12.2 min.	124.3 min.	184.8 min.	24.8 min.	25.6 min.	208.2 min.	8.3
D8754.8.81b	16.1 min.		9.4 min.			76.9 min.		-	-	100.9 min.	-
D8754.8.82b	10.5 min.		9.7 min.			61.7 min.		-	-	67.9 min.	-
D8754.8.90b	22 min.	25.3 min.	11.9 min.	8.3 min. (RHS)	16.6 min.	140 min.	300.6 min.	18.3 min.	25.4 min.	281.1 min.	-
D8754.8.98a	41.9 min.	42.1 min.	15.5			430.6 min.	451.1 min.	40.5 min.	42.1 min.	435 min.	-
D8754.8.98b	24.7 min.	28.3 min.	20 min.	19.2 min. (LHS)	38.4 min.	285.8 min.	808.2 min.	24.7 min.	28.3 min.	724.5 min.	-
D8754.8.98c	41.1		15.5 min.	11.7 min. (RHS)	23.4 min.	245.2 min.	491.2 min.	41.1		641.2 min.	-
D8754.8.98d	33.8 min.	25 min.	13.3 min.	8.7 min. (RHS)	17.4 min.	167.3 min.	262.4 min.	24.3 min.	25 min.	290 min.	9.6
D8754.8.100a	53.2 min.	55.4 min.	42.5 min.	24.9 min. (LHS)	49.8 min.	1188.1 min.	1875.4 min.	47 min.	55.4 min.	1839.3 min.	-
D8754.8.101a	40.2 min.	45.1 min.	38.4 min.	25.1 min. (RHS)	50.2 min.	662.9 min.	1791 min.	8.2	45.1 min.	1509.3 min.	-
D8754.8.101a	37.5 min.		46.1 min.	46.1 min. (RHS)	92.2 min.	679.8 min.	1359.6 min.	-	-	2305 min.	-

Table A2-4 Santa Marta Formation leaf measurements.

Specimen Number	Maximum length (mm)		Maximum width (mm)		Max. width one half (mm)		Max. width est. (mm)		Area (sq. mm)		Max. length est. (mm)		Area est. (sq. mm)		Max. length along primary (mm)		Max. length along primary est. (mm)		Leaf area (sq. mm)		Petiole length (mm)
D8604.37Aa	29.2	min.	17.1		-		-		266.6	min.	-		-		28.6	min.	-		-		-
D8604.37A/Ca	36.0	min.	17.0		-		-		326.3	min.	38.9	min.	548	min.	30.6	min.	39.1	min.	443.1	min.	-
D8604.37Ba	38.6	min.	18.9		-		-		395.2	min.	41.0	min.	620.6	min.	33.1	min.	41.3	min.	520.4	min.	-
D8604.37A/Ca&Ba	37.3	min.	18.0		-		-		360.8	min.	40.0	min.	584.3	min.	31.9	min.	40.2	min.	481.8	min.	-
D8604.38Aa	25.6	min.	13.1	min.	6.7	min. (RHS)	13.4	min.	196.2	min.	25.9	min.	270.4	min.	20.9	min.	26	min.	232.3	min.	-
D8604.38Ba	22.7	min.	13.9	min.	8	min. (RHS)	16	min.	156.6	min.	22.8	min.	225.6	min.	18.9	min.	22.9	min.	244.3	min.	-
D8604.38Aa&Ba	24.2	min.	13.9	min.	8	min. (RHS)	16	min.	176.4	min.	24.4	min.	248.0	min.	19.9	min.	24.5	min.	238.3	min.	-
D8604.39a	30.9	min.	25.1	min.	16	(RHS)	32		398.9	min.	32.8	min.	764.8	min.	19.4	min.	32.8	min.	699.7	min.	-
D8604.54a	38.1	min.	15.4	min.	7.7	min. (LHS)	15.4	min.	356.7	min.	43.6	min.	427	min.	38.1	min.	43.8	min.	449.7	min.	-
D8605.1Aa	93.1	min.	22.9	min.	20.4	(RHS)	40.8		1272.2	min.	96.5	min.	2930	min.	67.3	min.	96.7	min.	2630.2	min.	-
D8605.1Ba	95.0	min.	24.1	min.	20.7	(LHS)	41.4		1359.8	min.	98.8	min.	3129.4	min.	70.8	min.	99.3	min.	2740.7	min.	-
D8605.1A&Ba	94.1	min.	23.5	min.	20.6		41.1		1316.0	min.	97.7	min.	3029.7	min.	69.1	min.	98.0	min.	2685.2	min.	-
D8605.2a	46.7	min.	11.7	min.	10.4	(LHS)	20.8		357.9	min.	47.4	min.	746	min.	33.2	min.	47.4	min.	657.3	min.	-
D8605.5a	17.6	min.	15.3	min.	7.7	min. (LHS)	15.4	min.	148.7	min.	23.4	min.	316.6	min.	15.2	min.	23.4	min.	240.2	min.	-
D8605.15a	20.0	min.	15.7	min.	7.8	min. (RHS)	15.6	min.	161.7	min.	24.0	min.	321.2	min.	14.6	min.	24	min.	251.2	min.	-
D8605a&15a	20.0	min.	15.7	min.	7.8	min.	15.6	min.	161.7	min.	24.0	min.	321.2	min.	14.9	min.	24	min.	251.2	min.	-
D8605.7a	11.5	min.	11.0	min.	11	min. (LHS)	22	min.	62.6	min.	-		125.2	min.	-		-		168.7	min.	-
D8605.8Aa	26.9	min.	15.1	min.	14.8	min. (LHS)	29.6	min.	257.2	min.	28.7	min.	614.8	min.	21.0	min.	28.7	min.	566.3	min.	-
D8605.8Ba	27.7	min.	14.8	min.	14.6	min. (RHS)	29.2	min.	258.1	min.	30.2	min.	631.2	min.	21.6	min.	30.2	min.	587.9	min.	-
D8605.8Aa&8Ba	27.3	min.	15.0	min.	14.7	min.	29.4	min.	257.7		29.5	min.	623.0	min.	21.3	min.	29.5	min.	577.2	min.	-
D8605.14a	44.5	min.	18.9	min.	18.9	min. (LHS)	37.8	min.	404.2	min.	-		808.4	min.	-		-		1121.4	min.	-
D8605.16a	36.0	min.	27.9	min.	27.5	min. (LHS)	55	min.	607.8	min.	42.4	min.	1703.2	min.	17.1	min.	42.5	min.	1558.3	min.	-
D8605.19Aa	37.0	min.	8.9	min.	6.5	min. (LHS)	13	min.	159.0	min.	37.3	min.	273.8	min.	36.6	min.	37.3	min.	323.3	min.	-
D8605.20a	14.5	min.	8.2	min.	8.2	min. (RHS)	16.4	min.	84.9	min.	-		169.8	min.	-		-		158.5	min.	-
D8605.21Aa	38.5	min.	27.6	min.	15.3	min. (LHS)	30.6	min.	436.3	min.	51.2	min.	1054.6	min.	31.7	min.	51.2	min.	1044.5	min.	-
D8605.21Ba	49.7	min.	32.9	min.	16.7	min. (LHS)	33.4	min.	788.4	min.	51.0	min.	1020.8	min.	40.9	min.	51.1	min.	1137.8	min.	-
D8605.21Aa&21Ba	49.7	min.	32.9	min.	16.7	min. (LHS)	33.4	min.	788.4	min.	51.1	min.	1037.7	min.	40.9	min.	51.2	min.	1138.9	min.	-
D8605.22Ba	5.3	min.	5.7	min.	3	min. (RHS)	6	min.	21.0	min.	6.3	min.	27.6	min.	5.1	min.	6.3	min.	25.2	min.	-
D8605.24a	12.4	min.	8.9	min.	8.9	min. (LHS)	17.8	min.	60.2	min.	-		120.4	min.	-		-		147.1	min.	-
D8605.26a	21.7	min.	12.2	min.	8	min. (RHS)	16	min.	149.8	min.	23.3	min.	275.4	min.	19.3	min.	23.3	min.	248.5	min.	-
D8605.27Aa	19.9	min.	15.2	min.	15.2	min. (RHS)	30.4	min.	156.7	min.	-		313.4	min.	-		-		403.3	min.	-
D8605.27Ba	19.8	min.	15.2	min.	15.2	min. (LHS)	30.4	min.	159.0	min.	-		318.0	min.	-		-		401.3	min.	-
D8605.27Aa&Ba	19.9	min.	15.2	min.	15.2	min.	30.4	min.	157.9	min.	-		315.7	min.	-		-		402.3	min.	-
D8605.28a	12.6	min.	9.1	min.	5.9	min. (RHS)	11.8	min.	50.6	min.	13.0	min.	86.4	min.	11.9	min.	13	min.	102.3	min.	-
D8605.29a	26.2	min.	27.1	min.	27.1	min.	54.2	min.	402.1	min.	-		804.2	min.	-		-		946.7	min.	-
D8605.30a	61.0	min.	28.6		-		-		1155.8	min.	64.8	min.	1255	min.	57.0	min.	64.9	min.	1237.4	min.	-
D8605.31a	44.0	min.	26.8	min.	18.3	min. (LHS)	36.6	min.	618.8	min.	46.5	min.	1396.8	min.	32.8	min.	46.6	min.	1137.0	min.	-
D8605.33a	38.5	min.	12.6	min.	7	min. (LHS)	14	min.	322.6	min.	39.1	min.	397.8	min.	37.9	min.	39.1	min.	364.9	min.	-
D8606.4Aa	21.3	min.	14.5	min.	10.1	min. (LHS)	20.2	min.	203.8	min.	23.3	min.	336	min.	20.7	min.	23.4	min.	315.1	min.	-
D8606.4Ba	21.1	min.	14.6	min.	10.3	min. (RHS)	20.6	min.	187.3	min.	22.9	min.	339.4	min.	20.5	min.	22.9	min.	314.5	min.	-
D8606.4Aa&Ba	21.2	min.	14.6	min.	10.2	min.	20.4	min.	203.8	min.	23.1	min.	337.7	min.	20.6	min.	23.2	min.	314.8	min.	-
D8606.5a	14.4	min.	5.5		-		-		49.9	min.	14.6	min.	51.8	min.	14.3	min.	14.6	min.	53.5	min.	3.4

Table A2-4 Santa Marta Formation leaf measurements.

Appendix Two

Specimen Number	Maximum length (mm)		Maximum width (mm)		Max. width one half (mm)		Max. width est. (mm)		Area (sq. mm)		Max. length est. (mm)		Area est. (sq. mm)		Max. length along primary (mm)		Max. length along primary est. (mm)		Leaf area (sq. mm)		Petiole length (mm)
D8606.6a	16.9	min.	12.3	min.	7.7	min. (LHS)	15.4	min.	112.8	min.	17.7	min.	193.2	min.	13.5	min.	17.8	min.	182.7	min.	-
D8606.7Aa	57.8	min.	16.2	min.	-		-		722.3	min.	60.9	min.	778.2	min.	56.0	min.	60.9	min.	657.7	min.	-
D8606.7Ba	58.5	min.	16.0		-		-		710.2	min.	60.9	min.	757	min.	56.7	min.	60.9	min.	649.6	min.	-
D8606.7Aa&Ba	58.2	min.	16.1		-		-		716.3	min.	60.9	min.	767.6	min.	56.4	min.	60.9	min.	653.7	min.	-
D8606.8a	29.5	min.	29.3	min.	14.8	min. (LHS)	29.6	min.	550.8	min.	37.2	min.	955.2	min.	25.9	min.	37.3	min.	736.1	min.	-
D8609.147a	22.7	min.	9.6	min.	-		-	min.	142.6	min.	23.8	min.	172.6	min.	21.6	min.	24	min.	153.6	min.	-
D8610.1Aa	47.6	min.	36.0	min.	18.3	min. (LHS)	36.6	min.	896.1	min.	52.1	min.	1454.4	min.	33.1	min.	52.1	min.	1271.2	min.	-
D8610.1Ba	47.4	min.	35.9	min.	18.8	min. (RHS)	37.6	min.	902.3	min.	51.5	min.	1504.4	min.	35.2	min.	51.5	min.	1290.9	min.	-
D8610.1Aa&Ba	47.5	min.	36.0	min.	18.6	min.	37.1	min.	899.2	min.	51.8	min.	1479.4	min.	34.2	min.	51.8	min.	1281.2	min.	-
D8616.74a	24.0		16.1		-		-		203.7		-		-		23.5		-		256.3		-
D8616.128a	46.5	min.	38.5	min.	20	min. (RHS)	40	min.	864.4	min.	50.3	min.	1511	min.	26.4	min.	50.3	min.	1341.3	min.	-
D8618.106a	63.0	min.	34.2	min.	18.3	(RHS)	36.6		1512.9	min.	63.4	min.	1798.6	min.	59.6	min.	63.8	min.	1556.7	min.	2.8
D8619.6a	47.7	min.	38.5		-		-		1088.0	min.	47.8	min.	1256.2	min.	45.7	min.	48	min.	1232.0	min.	-
D8619.7a	42.4	min.	28.4	min.	15.1	min. (LHS)	30.2	min.	837.5	min.	54.2	min.	1235.2	min.	38.0	min.	54.2	min.	1091.2	min.	-
D8619.12a	50.1	min.	70.0	min.	36.9	min. (RHS)	73.8	min.	1691.3	min.	52.0	min.	2324	min.	45.8	min.	52.2	min.	2568.2	min.	-
D8619.18a	69.0	min.	33.3		-		-		1471.7	min.	69.8	min.	1572.8	min.	62.8	min.	69.8	min.	1549.6	min.	-
D8621.27a	51.4	min.	38.7	min.	-		-		1218.5	min.	58.7	min.	1692	min.	40.4	min.	58.7	min.	1514.5	min.	-
D8625.119a	55.9	min.	35.3	min.	23.2	min. (LHS)	46.4	min.	1076.8	min.	58.6	min.	1937.4	min.	40.5	min.	58.4	min.	1379.1	min.	-
DJ134.2Aa	18.1	min.	13.8	min.	7.3	min. (RHS)	14.6	min.	128.6	min.	19.8	min.	161	min.	17.2	min.	19.8	min.	192.7	min.	-
DJ134.2Ba	17.4	min.	13.5	min.	7	min. (LHS)	14	min.	125.6	min.	21.2	min.	174.4	min.	16.7	min.	21.2	min.	197.9	min.	-
DJ134.2Aa&Ba	17.8	min.	13.7	min.	7.2	min.	14.3	min.	127.1	min.	20.5	min.	167.7	min.	17.0	min.	20.5	min.	195.4	min.	-
DJ134.6a	14.0	min.	10.6	min.	6.6	min. (RHS)	13.2	min.	76.2	min.	14.1	min.	108.4	min.	14.0	min.	14.2	min.	125.0	min.	-
DJ134.11a	17.7	min.	10.6	min.	7.4	min. (LHS)	14.8	min.	65.1	min.	18.2	min.	175.8	min.	17.7	min.	18.2	min.	179.6	min.	-
DJ134.12Aa	15.4	min.	11.3	min.	-		-		112.7	min.	-		-		-		-		116.0	min.	-
DJ134.12Ba	14.9	min.	11.5	min.	-		-		116.4	min.	-		-		-		-		114.2	min.	-
DJ134.12A&Ba	15.2	min.	11.4	min.	-		-		114.6	min.	-		-		-		-		115.1	min.	-
DJ134.13a	31.7	min.	24.6	min.	12.7	min. (RHS)	25.4	min.	557.8	min.	32.0	min.	634	min.	28.3	min.	31.2	min.	541.9	min.	-
DJ134.15Aa	69.8		18.0		-		-		742.6	min.	-		790.2		70.0		-		837.6		-
DJ134.15Ba	69.7		18.4		-		-		765.5	min.	-		792.2		68.7		-		855.0		-
DJ134.15Aa&Ba	69.8		18.2		-		-		754.1	min.	-		791.2		69.4		-		846.3		-
DJ134.16a	39.0	min.	24.8	min.	16.8	min. (RHS)	33.6	min.	553.2	min.	40.7	min.	858.6	min.	34.8	min.	40.8	min.	913.9	min.	14.2
DJ134.21A/Ba	33.7	min.	32.8	min.	23.6	min. (LHS)	47.2	min.	513.7	min.	35.0	min.	1205.8	min.	28.9	min.	35.2	min.	1107.6	min.	1
DJ134.22A/Ba	66.6	min.	59.5	min.	-		-		2029.7	min.	66.6	min.	2443.2	min.	40.6	min.	64.6	min.	2641.8	min.	-
DJ134.27Ba	64.7	min.	46.6	min.	24.5	min. (RHS)	49	min.	2023.9	min.	65.4	min.	2638.6	min.	55.4	min.	65.5	min.	2139.7	min.	-
DJ134.28Aa	35.6	min.	15.0	min.	15	min. (LHS)	30	min.	317.4	min.	-		634.8	min.	-		-		712.0	min.	-
DJ147.1a	10.9	min.	6.5	min.	3.6	min. (LHS)	7.2	min.	40.1	min.	13.2	min.	50.8	min.	10.1	min.	13.1	min.	63.4	min.	-
DJ147.3a	13.9	min.	10.0	min.	-		-		71.8	min.	-		-		-		-		92.7	min.	-
DJ147.4a	30.8	min.	15.8	min.	15.6	min. (LHS)	31.2	min.	144.2	min.	32.0	min.	673.4	min.	4.3	min.	32	min.	665.6	min.	-
DJ147.6a	23.9	min.	13.8	min.	7.3	(RHS)	14.6		229.8	min.	24.1	min.	271	min.	23.6	min.	24.2	min.	235.5	min.	-
DJ147.7a	40.2	min.	12.7	min.	11.7	min. (RHS)	23.4	min.	367.9	min.	41.4	min.	858.2	min.	32.2	min.	41.4	min.	645.8	min.	-
DJ147.8a	24.1	min.	8.4	min.	8.4	min. (LHS)	16.8	min.	118.6	min.	-		237.2	min.	-		-		269.9	min.	-
DJ147.9a	25.7	min.	19.0	min.	-		-		218.9	min.	25.9	min.	303.4	min.	25.8	min.	26	min.	329.3	min.	-

Table A2-4 Santa Marta Formation leaf measurements.

Specimen Number	Maximum length (mm)	Maximum width (mm)	Max. width one half (mm)	Max. width est. (mm)	Area (sq. mm)	Max. length est. (mm)	Area est. (sq. mm)	Max. length along primary (mm)	Max. length along primary est. (mm)	Leaf area (sq. mm)	Petiole length (mm)
DJ147.15a	19.4 min.	18.5 min.	-	-	207.7 min.	23.1 min.	265 min.	19.0 min.	23.2 min.	286.1 min.	-
DJ147.9a&15a	25.7 min.	19.0 min.	-	-	218.9 min.	25.9 min.	303.4 min.	25.8 min.	26 min.	329.3 min.	-
DJ147.10a	32.2 min.	12.0 min.	-	-	219.0 min.	32.4 min.	262.3 min.	31.3 min.	32.5 min.	260.0 min.	-
DJ147.11a	38.3 min.	11.1 min.	7.6 min. (RHS)	15.2 min.	245.7 min.	38.5 min.	365.6 min.	37.5 min.	38.5 min.	390.1 min.	-
DJ147.12Aa	23.3	7.6	-	-	108.1 min.	-	111	23.3	-	118.1	-
DJ147.12Ba	23.8	8.1	-	-	121.6 min.	-	122	23.9	-	129.1	-
DJ147.12Aa&Ba	23.6	7.9	-	-	114.9 min.	-	116.5	23.6	-	123.5	-
DJ147.13a	27.0 min.	18.9 min.	-	-	288.7 min.	-	-	-	-	340.2 min.	-
DJ147.14a	33.3 min.	17.2 min.	-	-	305.2 min.	34.4 min.	337.2 min.	32.1 min.	34.3 min.	394.5 min.	-
DJ147.17a	38.9 min.	17.0 min.	9.7 min. (LHS)	19.4 min.	290.4 min.	39.0 min.	595.4 min.	34.7 min.	35.2 min.	504.4 min.	-
DJ147.18a	18.4 min.	9.0 min.	9 min. (RHS)	18 min.	84.4 min.	-	168.8 min.	-	-	220.8 min.	-
DJ147.19a	49.1 min.	11.1 min.	8.7 (RHS)	17.4	302.6 min.	49.9 min.	633.6 min.	49.9 min.	50.8 min.	589.3 min.	-
DJ147.54a	40.6 min.	10.6 min.	8.6 min. (LHS)	17.2 min.	234.4 min.	40.9 min.	497.8 min.	38.3 min.	41.1 min.	471.3 min.	-
DJ147.19a&54a	49.1 min.	11.1 min.	8.7	17.4	302.6 min.	49.9 min.	633.6 min.	49.9 min.	50.8 min.	589.3 min.	-
DJ147.20a	21.8 min.	17.2 min.	11 min. (RHS)	22 min.	234.4 min.	22.3 min.	349.8 min.	19.6 min.	21.4 min.	327.1 min.	-
DJ147.23a	17.8 min.	12.1 min.	-	-	118.9 min.	19.1 min.	176.8 min.	13.6 min.	19.1 min.	154.1 min.	-
DJ147.24a	15.4 min.	9.0 min.	4.6 min. (LHS)	9.2 min.	96.4 min.	17.9 min.	126.2 min.	14.6 min.	17.9 min.	109.8 min.	-
DJ147.25a	28.1 min.	21.0 min.	11.8 (LHS)	23.6	393.9 min.	28.8 min.	578.6 min.	21.2 min.	29 min.	456.3 min.	-
DJ147.26a	17.5 min.	14.3 min.	14.3 min. (LHS)	28.6 min.	143.0 min.	-	286 min.	-	-	333.7 min.	-
DJ147.28a	17.2 min.	14.2 min.	-	-	136.6 min.	-	-	-	-	162.8 min.	-
DJ147.29a	15.3 min.	7.8 min.	7.8 min. (LHS)	15.6 min.	76.1 min.	-	152.2 min.	-	-	159.1 min.	-
DJ147.30a	21.3 min.	12.5 min.	12.5 min. (LHS)	25 min.	163.8 min.	25.2 min.	443.2 min.	17.5 min.	25.3 min.	421.7 min.	-
DJ147.31a	20.0 min.	12.7 min.	12.1 min. (RHS)	24.2 min.	188.5 min.	22.9 min.	459.6 min.	12.3 min.	22.9 min.	369.5 min.	-
DJ147.32a	51.5 min.	22.2 min.	12.5 min. (LHS)	24.9 min.	611.9 min.	51.6 min.	841 min.	50.6 min.	51.7 min.	857.4 min.	-
DJ147.33a	21.0 min.	9.0 min.	8.4 min. (RHS)	16.8 min.	113.1 min.	21.8 min.	228.6 min.	20.4 min.	21.8 min.	244.2 min.	-
DJ147.34a	31.8 min.	12.5 min.	12.5 min. (LHS)	25 min.	152.4 min.	-	304.8 min.	-	-	530.0 min.	-
DJ147.35a	23.3 min.	17.5 min.	9.9 min. (RHS)	19.8 min.	244.1 min.	24.8 min.	388 min.	13.6 min.	24.8 min.	327.4 min.	-
DJ147.37Aa	31.5 min.	25.3 min.	13.3 (LHS)	26.6	574.3 min.	32.1 min.	607.4 min.	32.0 min.	32.5 min.	576.3 min.	-
DJ147.37B/Ca	33.2 min.	24.4 min.	12.4 (RHS)	24.8	581.5 min.	33.6 min.	609.2 min.	32.4 min.	33.9 min.	560.5 min.	-
DJ147.37A&B/Ca	32.3 min.	24.9 min.	12.9 min.	25.7	577.9 min.	32.9 min.	608.3 min.	32.2 min.	33.2 min.	568.8 min.	-
DJ147.38Aa	46.1 min.	11.8 min.	10.5 (RHS)	21	327.9 min.	49.2 min.	725.2 min.	46.1 min.	49.3 min.	690.2 min.	-
DJ147.39a	30.4	12.8 min.	8.5 (LHS)	17	161.6 min.	-	247	30.4	-	344.5	3.8
DJ147.40a	36.0 min.	16.2 min.	13 min. (RHS)	26 min.	323.9 min.	36.9 min.	721.2 min.	29.1 min.	37 min.	641.3 min.	-
DJ147.41Aa	19.6 min.	7.0 min.	6.7 min. (LHS)	13.4 min.	87.9 min.	20.6 min.	206 min.	7.6 min.	20.6 min.	184.0 min.	-
DJ147.43a	14.9 min.	17.2 min.	10.5 min. (RHS)	21 min.	137.1 min.	15.5 min.	235.2 min.	14.3 min.	15.6 min.	218.4 min.	-
DJ147.44a	35.2	11.1 min.	6.6 (LHS)	13.2	139.7 min.	-	214.6	35.8	-	315.0	0.5
DJ147.45a	26.3 min.	24.4 min.	14.5 min. (RHS)	29 min.	341.2 min.	27.3 min.	528 min.	21.3 min.	26.2 min.	527.8 min.	-
DJ147.46a	48.3 min.	18.0 min.	9.1 min. (LHS)	18.2 min.	479.5 min.	48.6 min.	500.2 min.	47.6 min.	48.7 min.	590.9 min.	-
DJ147.48a	16.6 min.	17.2 min.	13.6 min. (RHS)	27.2 min.	141.5 min.	17.4 min.	335.4 min.	11.1 min.	17.4 min.	315.5 min.	1.9
DJ147.49A&Ba	24.9 min.	35.1 min.	24.4 min. (RHS)	48.8 min.	469.6 min.	25.8 min.	973.2 min.	14.2 min.	25.3 min.	839.4 min.	1.7
DJ147.51a	21.3 min.	14.4 min.	11 min. (LHS)	22 min.	161.2 min.	21.3 min.	316.4 min.	20.3 min.	21.3 min.	312.4 min.	-
DJ147.52a	24.5 min.	10.3 min.	9.8 min. (LHS)	19.6 min.	152.9 min.	25.2 min.	326 min.	22.7 min.	25.2 min.	329.3 min.	-
DJ147.53a	30.4 min.	27.6 min.	17 (LHS)	34	456.9 min.	32.0 min.	592 min.	29.0 min.	31.8 min.	725.3 min.	-

Table A2-4 Santa Marta Formation leaf measurements.

Specimen Number	Maximum length (mm)		Maximum width (mm)		Max. width one half (mm)		Max. width est. (mm)		Area (sq. mm)		Max. length est. (mm)		Area est. (sq. mm)		Max. length along primary (mm)		Max. length along primary est. (mm)		Leaf area (sq. mm)		Petiole length (mm)
DJ147.55Aa	39.5	min.	17.7	min.	10.5	min. (LHS)	21	min.	312.7	min.	39.5	min.	568.8	min.	28.9	min.	39.5	min.	553.0	min.	-
DJ147.55Ba	39.3	min.	17.9	min.	10.8	min. (RHS)	21.6	min.	302.2	min.	39.5	min.	583	min.	26.2	min.	39.5	min.	568.8	min.	-
DJ147.55A&Ba	39.4	min.	17.8	min.	10.7	min.	21.3	min.	312.7	min.	39.5	min.	575.9	min.	27.6	min.	39.5	min.	560.9	min.	-
DJ147.56a	32.7	min.	10.6	min.	9.8	min. (RHS)	19.6	min.	188.7	min.	33.0	min.	394	min.	29.9	min.	33.1	min.	432.5	min.	-
DJ147.59a	19.8	min.	15.0	min.	8.3	min. (RHS)	16.6	min.	157.5	min.	20.4	min.	243	min.	19.6	min.	20.5	min.	226.9	min.	-
DJ147.60a	20.2	min.	9.1	min.	9	min. (LHS)	18	min.	60.6	min.	23.2	min.	285.2	min.	8.6	min.	23.2	min.	278.4	min.	-
DJ147.60b	15.4	min.	13.3	min.	10.1	min. (RHS)	20.2	min.	150.4	min.	21.8	min.	344.8	min.	14.0	min.	21.8	min.	293.6	min.	-
DJ451.7a	50.8	min.	33.7	min.	17	min. (RHS)	34	min.	999.8	min.	67.0	min.	1712.8	min.	45.7	min.	67.1	min.	1520.9	min.	-
DJ452.2a	21.0	min.	9.5	min.	4.9	min. (RHS)	9.8	min.	89.9	min.	21.4	min.	103.8	min.	18.2	min.	21.4	min.	139.8	min.	-

Specimen number	b_1	b_2	b_3	m_4	m_5	m_6	m_7	b_8	m_9	m_10	m_11	12	13	m_14	b_15	m_16	b_17	b_18	b_19	b_20	21	21	23
D8754.8.1a	nc	nc	0	3	3	7	4	0	8	3	2	73	63	4	1	3	0	0	0	0	80	86	95
D8754.8.2a&3a avg.	1	1	0	3	3	5	4	0	8	2	2	75	75	6	1	3	0	0	0	0	87	84	82
D8754.8.4a&5a avg.	nc	nc	0	nc	nc	nc	nc	nc	8	3	1	58	nc	3	0	3	1	0	1	nc	88	72	72
D8754.8.4b&5b avg.	nc	nc	nc	nc	nc	nc	nc	nc	4	2	1	63	nc	nc	0	3	1	0	1	nc	79	83	69
D8754.8.4c	nc	nc	nc	nc	nc	nc	nc	0	8	4	1	53	47	2	1	2	1	0	nc	0	90	74	97
D8754.8.4d	nc	nc	nc	nc	nc	4	3	nc	nc	nc	1	nc	37	nc	nc	nc	nc	0	nc	0	77	62	87
D8754.8.5d	nc	0	0	nc	nc	3	1	1	4	1	1	49	62	nc	0	nc	nc	0	0	0	nc	nc	nc
D8754.8.6a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	1	70	nc	nc	nc	nc	nc	0	0	nc	87	87	nc
D8754.8.6b&65a	nc	nc	nc	nc	nc	nc	5	nc	1	2	2	61	nc	nc	0	2	0	0	1	0	93	76	103
D8754.8.7a	nc	nc	nc	nc	nc	2	nc	nc	nc	nc	nc	72	nc	nc	nc	3	1	0	nc	nc	80	84	nc
D8754.8.8a&9a avg.	1	1	1	3	1	4	3	0	1	2	2	53	51	6	1	3	0	0	1	0	94	98	119
D8754.8.8b	nc	nc	nc	nc	nc	4	3	0	nc	nc	1	nc	38	nc	nc	nc	nc	0	0	0	73	76	nc
D8754.8.11b	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	92	80	nc
D8754.8.14b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	3	1	0	nc	nc	nc	nc	nc	nc
D8754.8.15a	nc	nc	nc	nc	nc	nc	1	nc	4	2	1	87	nc	nc	1	3	0	0	1	nc	75	92	nc
D8754.8.16a	nc	nc	nc	nc	nc	nc	nc	1	nc	nc	1	77	64	6	1	nc	1	0	nc	0	73	64	87
D8754.8.16b	nc	nc	nc	nc	nc	6	1	1	7	2	1	nc	66	nc	1	3	0	0	0	0	90	82	89
D8754.8.16e	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8754.8.16f	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8754.8.17b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	2	58	nc	nc	1	3	0	0	0	0	88	67	75
D8754.8.17c	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8754.8.21a&46e	1	nc	nc	nc	nc	nc	nc	nc	4	1	1	79	nc	6	0	3	1	0	1	nc	91	107	59
D8754.8.22a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	2	43	nc	nc	1	nc	nc	0	0	0	nc	nc	nc
D8754.8.22b	nc	nc	nc	nc	nc	nc	4	nc	4	1	nc	71	nc	1	0	3	0	0	0	0	97	68	97
D8754.8.24b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8754.8.25a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	73	74	nc
D8754.8.26a	nc	nc	nc	nc	nc	nc	nc	nc	4	nc	nc	28	nc	nc	0	nc	nc	0	nc	0	81	100	59
D8754.8.26c	nc	nc	nc	nc	nc	2	nc	0	nc	1	1	47	nc	nc	nc	3	0	0	0	0	nc	nc	nc
D8754.8.27a	nc	nc	nc	nc	nc	nc	nc	nc	3	2	nc	89	nc	nc	nc	3	0	0	nc	0	93	98	93
D8754.8.28a	nc	nc	nc	nc	nc	3	4	0	3	2	1	56	38	2	1	3	1	0	1	0	101	61	86
D8754.8.30a	nc	nc	nc	nc	nc	nc	4	nc	2	2	2	73	nc	6	1	3	1	1	1	0	88	75	72
D8754.8.31a	nc	nc	nc	nc	nc	nc	4	nc	2	2	1	76	nc	6	1	3	1	0	1	0	96	69	105
D8754.8.32a&98e	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	65	nc	nc	nc	2	1	0	nc	0	75	67	nc
D8754.8.33a	1	1	nc	nc	nc	3	1	1	5	1	1	56	25	4	0	3	1	0	0	0	82	77	nc
D8754.8.34a	nc	nc	nc	nc	nc	nc	3	nc	1	2	1	68	nc	6	0	2	1	1	nc	0	106	88	80
D8754.8.34b	1	nc	nc	nc	nc	nc	4	nc	nc	3	2	88	nc	6	1	4	1	0	nc	0	91	87	96
D8754.8.35a&37a	1	0	nc	3	nc	4	1	1	4	2	1	62	nc	6	0	3	1	0	nc	0	84	74	101
D8754.8.36a	1	1	nc	1	nc	3	1	1	4	2	2	68	44	6	1	3	0	0	0	nc	110	51	nc
D8754.8.38a	1	nc	nc	nc	nc	nc	1	nc	nc	2	1	58	nc	nc	1	3	1	0	1	nc	77	69	54
D8754.8.38b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8754.8.39a	0	0	0	3	2	6	1	0	4	2	2	84	69	6	1	3	0	0	nc	0	85	52	nc
D8754.8.39b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	74	nc	nc	nc	3	0	0	nc	nc	nc	nc	nc
D8754.8.40a	1	1	nc	1	nc	3	1	1	5	3	2	58	79	6	0	3	1	0	1	0	94	81	81
D8754.8.41a	1	nc	nc	3	nc	2	1	0	5	2	2	48	40	6	0	3	1	0	1	0	81	89	83
D8754.8.42a	nc	nc	nc	3	nc	nc	1	nc	4	2	1	75	56	4	0	3	1	0	1	0	88	83	85
D8754.8.43a	nc	nc	nc	nc	nc	2	3	0	4	3	1	49	18	4	1	4	1	0	0	0	74	104	72
D8754.8.44a	1	0	nc	nc	nc	2	1	0	7	2	2	37	37	nc	1	3	nc	0	0	nc	97	71	73
D8754.8.44b	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	nc	nc	nc	nc	4	1	1	nc	nc	nc	nc	nc
D8754.8.45a	1	1	nc	4	1	3	1	1	4	2	1	54	26	4	1	3	1	0	nc	nc	94	71	74
D8754.8.45b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	3	nc	0	nc	nc	80	61	69
D8754.8.46a	1	1	nc	nc	nc	3	1	1	4	2	1	49	46	6	1	3	1	0	1	nc	106	63	82
D8754.8.46d	1	nc	1	nc	nc	nc	4	nc	1	1	2	39	nc	6	1	4	1	1	nc	0	85	87	nc
D8754.8.47a	nc	nc	nc	nc	nc	nc	nc	nc	nc	2	1	44	nc	3	nc	2	0	0	0	0	75	85	84
D8754.8.47b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	1	40	nc	nc	1	nc	nc	0	nc	0	95	84	nc
D8754.8.47c	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	3	nc	0	nc	nc	nc	nc	nc
D8754.8.48a	nc	nc	nc	nc	nc	nc	nc	nc	4	2	2	54	nc	4	0	3	1	0	1	nc	78	102	78
D8754.8.48b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	85	71	nc
D8754.8.49a	nc	nc	nc	1	nc	2	nc	1	4	2	2	69	46	6	1	3	0	0	nc	0	66	42	nc
D8754.8.49b	nc	nc	nc	nc	nc	4	3	0	1	nc	1	nc	58	nc	nc	nc	nc	0	0	0	87	59	87
D8754.8.49c	nc	nc	nc	nc	nc	nc	4	nc	nc	nc	nc	nc	nc	nc	nc	1	1	0	0	nc	nc	nc	nc
D8754.8.50a	nc	nc	nc	nc	nc	2	nc	1	nc	1	1	61	50	6	1	2	0	0	nc	0	61	78	nc
D8754.8.50b	nc	nc	nc	nc	nc	nc	nc	nc	nc	2	2	50	nc	nc	nc	3	0	0	0	0	110	55	87
D8754.8.54a	nc	nc	nc	2	nc	2	1	0	7	2	2	52	26	4	0	3	0	0	0	nc	92	73	75
D8754.8.54b	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc	nc	nc	3	0	0	0	0	nc	73	nc

Table A3-1 Score sheet Hidden Lake Formation flora

'nc' - no comparison

Specimen number	b_1	b_2	b_3	m_4	m_5	m_6	m_7	b_8	m_9	m_10	m_11	12	13	m_14	b_15	m_16	b_17	b_18	b_19	b_20	21	21	23
D8754.8.56a	nc	nc	nc	nc	nc	3	nc	0	9	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8754.8.56b	nc	nc	nc	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	nc	nc	nc	0	0	nc	125	69	80
D8754.8.57a	1	0	nc	3	nc	2	1	0	7	1	2	54	40	4	1	3	0	0	0	0	88	74	70
D8754.8.58a	nc	nc	nc	nc	nc	7	4	nc	nc	nc	nc	nc	nc	nc	nc	3	0	0	0	0	93	66	nc
D8754.8.58b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	69	nc	nc	1	nc	nc	0	0	0	98	96	nc
D8754.8.59a	nc	nc	nc	nc	nc	nc	3	nc	nc	1	2	69	nc	nc	1	3	0	0	nc	0	119	71	76
D8754.8.59c	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	1	54	nc	nc	nc	nc	nc	0	nc	0	87	61	63
D8754.8.60a	nc	nc	nc	nc	nc	5	3	0	7	2	1	nc	40	nc	nc	3	0	0	0	0	85	73	77
D8754.8.60b	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	80	74	nc
D8754.8.61a	nc	nc	nc	nc	nc	nc	nc	nc	8	3	2	65	65	nc	0	3	nc	0	0	0	88	111	nc
D8754.8.62a&64a	1	1	nc	nc	nc	4	2	0	9	3	2	69	69	nc	nc	nc	nc	0	0	0	58	49	nc
D8754.8.63a	1	1	nc	3	2	nc	5	0	5	2	2	46	23	4	1	2	nc	0	1	0	82	83	81
D8754.8.66b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	1	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8754.8.67a	nc	nc	nc	nc	nc	nc	nc	nc	nc	3	2	58	nc	nc	nc	3	1	0	nc	0	91	70	76
D8754.8.67b	nc	nc	nc	3	nc	4	2	0	7	2	1	nc	20	nc	0	3	0	0	0	0	79	79	70
D8754.8.68a	nc	nc	nc	nc	nc	3	1	nc	nc	1	1	53	28	4	1	3	0	0	1	0	83	82	89
D8754.8.68b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	3	1	0	nc	nc	71	93	nc
D8754.8.71b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8754.8.71c	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8754.8.73b	nc	nc	nc	nc	nc	5	nc	1	nc	nc	nc	33	43	nc	nc	nc	nc	0	0	0	97	64	nc
D8754.8.76b	1	1	nc	nc	nc	3	1	1	nc	1	1	38	12	4	nc	nc	nc	0	nc	0	101	38	66
D8754.8.81b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	3	1	0	nc	nc	nc	nc	nc
D8754.8.82b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	3	nc	0	nc	nc	nc	nc	nc
D8754.8.90b	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	1	66	nc	nc	nc	3	1	0	0	nc	101	89	nc
D8754.8.98a	1	1	nc	2	nc	3	1	0	4	2	2	65	54	6	0	3	1	0	nc	nc	88	76	87
D8754.8.98b	nc	nc	nc	nc	nc	nc	1	nc	nc	3	1	49	nc	nc	nc	nc	nc	0	0	0	76	89	90
D8754.8.98c	nc	nc	nc	3	nc	4	nc	0	4	2	1	78	75	1	0	3	0	0	0	1	85	86	88
D8754.8.98d	nc	nc	nc	nc	nc	3	nc	1	nc	1	nc	34	49	nc	nc	nc	nc	0	nc	nc	59	107	nc
D8754.8.100a	nc	nc	nc	3	nc	7	4	0	8	3	2	57	45	2	1	3	nc	0	nc	0	83	74	92
D8754.8.101a	nc	nc	nc	nc	nc	nc	3	nc	1	nc	nc	nc	nc	nc	nc	2	1	1	nc	0	66	53	nc

Table A3-1 Score sheet Hidden Lake Formation flora

'nc' - no comparison

Specimen number	b_1	b_2	b_3	m_4	m_5	m_6	m_7	b_8	m_9	m_10	m_11	12	13	m_14	b_15	m_16	b_17	b_18	b_19	b_20	21	21	23
D8604.37A/Ca&Ba	1	nc	nc	1	nc	nc	1	nc	4	1	2	44	nc	6	1	3	1	0	0	0	80	87	73
D8604.38Aa&Ba	1	nc	1	nc	4	nc	1	nc	6	2	1	73	nc	6	0	3	1	0	1	0	92	79	84
D8604.39a	1	1	nc	nc	nc	3	1	0	nc	2	1	26	nc	nc	nc	4	1	1	0	0	nc	47	nc
D8604.54a	nc	nc	0	nc	3	nc	1	nc	4	1	nc	50	nc	1	0	3	1	0	1	0	67	110	75
D8605.1Aa&1Ba	nc	nc	nc	1	nc	2	1	nc	4	2	2	35	nc	2	nc	2	1	0	0	1	92	64	94
D8605.2a	nc	nc	nc	1	nc	2	1	0	4	1	1	44	43	1	nc	3	1	0	0	0	94	90	88
D8605.5a&15a	nc	nc	nc	nc	nc	nc	1	nc	nc	2	1	43	nc	nc	0	3	1	0	1	0	94	92	79
D8605.7a	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	nc	nc	nc	nc	2	nc	0	nc	nc	112	83	nc
D8605.8Aa&Ba	nc	nc	nc	nc	nc	nc	1	nc	nc	3	nc	74	nc	nc	nc	3	1	0	nc	0	90	82	69
D8605.14a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	3	nc	0	1	0	97	86	nc
D8605.16a	nc	nc	nc	nc	nc	nc	5	nc	nc	4	nc	63	nc	6	nc	3	1	1	0	0	87	78	101
D8605.19Aa	nc	0	nc	nc	nc	3	5	1	1	1	1	24	16	2	0	1	1	0	1	0	93	77	98
D8605.20a	nc	nc	nc	nc	nc	nc	1	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	99	103	nc
D8605.21Aa&Ba	nc	0	nc	nc	nc	3	1	0	4	1	1	39	30	6	0	2	1	1	0	1	80	77	92
D8605.22Ba	nc	nc	nc	nc	nc	nc	nc	nc	nc	2	nc	41	nc	1	0	4	1	1	0	0	98	77	109
D8605.24a	nc	nc	nc	nc	nc	nc	1	nc	nc	nc	nc	nc	nc	nc	nc	3	1	0	nc	nc	83	99	nc
D8605.26a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	38	nc	nc	1	3	nc	0	1	nc	90	91	80
D8605.27Aa&Ba	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	nc	nc	nc	nc	3	nc	0	nc	nc	86	72	nc
D8605.28a	nc	nc	nc	nc	nc	nc	nc	nc	nc	1	1	51	nc	nc	0	2	0	0	1	nc	85	43	nc
D8605.29a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	nc	nc	nc
D8605.30a	1	nc	nc	nc	1	nc	1	nc	4	2	1	53	nc	6	0	3	0	0	0	1	94	82	102
D8605.31a	nc	nc	nc	nc	nc	nc	nc	nc	6	2	1	61	nc	1	0	2	1	1	0	nc	106	57	80
D8605.33a	nc	0	nc	nc	nc	1	1	0	7	1	1	47	29	4	1	3	0	0	1	nc	91	69	70
D8606.4Aa&Ba	nc	nc	nc	nc	nc	nc	1	nc	nc	2	nc	57	nc	nc	0	3	0	0	0	nc	92	62	85
D8606.5a	1	1	nc	nc	nc	3	2	1	1	1	1	40	31	6	1	4	1	0	0	0	71	101	nc
D8606.6a	nc	nc	nc	nc	nc	nc	nc	nc	1	1	1	74	nc	6	1	3	0	0	0	0	105	78	nc
D8606.7Aa&7Ba	nc	nc	nc	1	nc	nc	3	nc	2	2	1	53	nc	6	0	3	1	0	1	0	82	79	68
D8606.8a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	49	nc	nc	1	2	0	0	0	nc	77	96	nc
D8609.147a	nc	nc	nc	1	nc	nc	1	nc	4	2	2	53	nc	6	1	4	1	0	1	0	78	95	76
D8610.1A&Ba	nc	nc	nc	nc	nc	nc	1	nc	5	2	1	47	nc	6	1	3	0	0	1	0	84	94	82
D8616.74a	0	0	0	2	1	1	3	0	1	2	2	51	37	4	1	2	0	0	0	0	62	80	76
D8616.128a	nc	nc	nc	nc	nc	nc	3	nc	1	nc	nc	36	nc	1	0	2	0	0	1	0	80	93	117
D8618.106a	1	0	1	nc	nc	1	1	1	4	2	2	46	40	6	0	3	1	0	0	0	97	76	83
D8619.6a	1	1	nc	nc	nc	1	3	0	1	2	nc	44	30	2	1	2	0	0	0	0	79	92	77
D8619.7a	1	nc	nc	nc	nc	nc	1	nc	4	2	nc	69	nc	3	1	3	1	0	0	0	92	95	77
D8619.12a	nc	0	nc	nc	nc	5	nc	0	9	4	nc	44	44	nc	1	nc	nc	0	0	0	85	82	98
D8619.18a	1	1	1	3	1	nc	1	nc	4	3	1	41	nc	6	0	3	1	0	0	0	97	74	95
D8621.27a	nc	nc	nc	nc	nc	nc	3	nc	1	4	1	35	nc	1	0	2	1	1	1	0	79	94	127
D8625.119a	1	1	nc	3	nc	nc	4	0	1	3	1	50	56	3	1	3	0	0	0	0	77	63	108
DJ134.2Aa&Ba	nc	nc	0	nc	3	nc	3	nc	2	2	nc	57	nc	6	nc	3	1	0	0	0	84	73	67
DJ134.6a	nc	0	nc	nc	nc	2	1	0	7	2	nc	nc	35	1	nc	1	0	0	0	nc	89	86	124
DJ134.11a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	41	nc	1	1	3	0	0	0	nc	94	87	111
DJ134.12Aa&Ba	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	81	86	nc
DJ134.13a	1	nc	1	nc	5	nc	3	nc	1	2	1	55	nc	1	0	2	0	0	1	0	113	48	70
DJ134.15Aa&Ba	0	0	0	2	3	1	3	0	2	2	1	61	41	6	0	3	1	0	0	0	71	58	92
DJ134.16a	nc	0	nc	nc	nc	2	1	1	5	2	2	40	12	2	0	1	0	0	1	nc	95	83	nc
DJ134.21A/Ba	1	1	nc	nc	nc	5	nc	1	9	4	1	43	nc	nc	1	nc	nc	nc	nc	0	102	62	112
DJ134.22A/Ba	nc	nc	nc	nc	nc	nc	nc	nc	1	3	1	27	31	1	0	2	0	0	0	0	92	69	nc
DJ134.27Ba	nc	nc	nc	nc	nc	nc	4	0	4	2	1	45	46	6	1	3	1	1	0	0	94	68	92
DJ134.28a	nc	nc	nc	nc	nc	2	3	0	2	nc	nc	nc	nc	nc	nc	3	1	0	0	0	72	90	nc
DJ147.1a	nc	nc	0	nc	3	nc	2	nc	nc	2	nc	33	nc	nc	1	2	nc	0	nc	nc	nc	nc	nc
DJ147.3a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
DJ147.4a	nc	nc	nc	nc	nc	3	3	0	7	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	81	nc
DJ147.6a	nc	nc	nc	nc	nc	4	1	0	6	1	1	69	94	6	0	3	1	0	1	0	87	72	75
DJ147.7a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	1	71	nc	1	nc	3	1	0	0	nc	96	77	90
DJ147.8a	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	nc	nc	nc	nc	3	1	0	nc	nc	103	93	nc
DJ147.9a&15a	nc	nc	0	nc	1	nc	1	nc	4	2	2	59	nc	6	0	3	1	0	0	0	83	82	76
DJ147.10a	1	1	nc	1	3	2	1	0	4	2	2	77	50	6	1	3	1	0	1	0	92	81	97
DJ147.11a	nc	nc	nc	nc	3	1	4	0	8	2	2	72	nc	2	0	3	0	0	0	0	80	99	83
DJ147.12Aa&Ba	nc	nc	0	3	3	3	1	0	4	2	1	65	36	4	0	3	1	0	1	0	97	67	89
DJ147.13a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	92	85	86
DJ147.14a	1	nc	1	1	1	nc	1	nc	4	2	2	85	nc	1	0	3	1	0	1	0	89	79	89
DJ147.17a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	82	nc	nc	1	3	0	0	1	0	95	68	88
DJ147.18a	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	nc	nc	nc	nc	1	0	0	0	0	92	87	nc
DJ147.19a&54a	nc	nc	nc	1	nc	1	1	0	4	2	2	80	98	6	nc	3	1	0	1	0	92	88	81

Table A3-2 Score sheet Santa Marta Formation flora

'nc' - no comparison

Specimen number	b_1	b_2	b_3	m_4	m_5	m_6	m_7	b_8	m_9	m_10	m_11	12	13	m_14	b_15	m_16	b_17	b_18	b_19	b_20	21	21	23
DJ147.20a	nc	nc	nc	nc	nc	7	4	0	8	2	1	nc	nc	nc	nc	nc	nc	nc	0	0	nc	nc	nc
DJ147.23a	nc	nc	nc	nc	nc	nc	4	nc	nc	2	1	81	nc	nc	0	3	0	0	0	nc	96	93	90
DJ147.24a	nc	nc	nc	nc	nc	nc	3	nc	2	1	1	66	nc	6	0	3	1	0	1	0	92	82	79
DJ147.25a	nc	nc	nc	nc	nc	4	1	nc	4	2	2	75	nc	6	0	3	1	0	1	0	84	78	80
DJ147.26a	nc	nc	nc	nc	nc	nc	1	nc	nc	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	96	76	nc
DJ147.28a	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
DJ147.29a	nc	nc	nc	nc	nc	nc	1	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc
DJ147.30a	nc	nc	nc	nc	nc	nc	3	nc	7	4	nc	nc	nc	nc	nc	3	1	nc	nc	0	80	82	80
DJ147.31a	nc	nc	nc	nc	nc	nc	nc	nc	4	2	nc	61	nc	nc	nc	3	1	0	0	0	85	82	61
DJ147.32a	1	1	nc	nc	3	5	1	0	4	2	2	52	56	6	0	3	1	0	1	0	89	87	90
DJ147.33a	nc	nc	nc	nc	nc	2	1	0	4	1	1	78	34	4	nc	3	1	0	0	0	94	79	nc
DJ147.34a	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	nc	nc	nc	nc	3	nc	nc	nc	nc	90	73	nc
DJ147.35a	nc	nc	nc	3	nc	nc	5	nc	1	2	1	62	nc	6	0	4	1	0	1	0	93	64	79
DJ147.37A&B/Ca	1	nc	1	2	4	nc	4	0	4	3	2	48	nc	6	1	3	1	1	1	0	83	78	86
DJ147.38Aa	nc	nc	nc	3	3	nc	1	nc	4	2	1	76	nc	2	nc	3	1	0	1	0	90	92	85
DJ147.39a	1	nc	1	3	3	1	2	1	4	1	2	48	47	6	0	3	1	0	1	0	87	83	60
DJ147.40a	nc	nc	nc	nc	nc	nc	1	nc	4	2	2	72	nc	6	0	3	1	0	1	0	77	71	90
DJ147.41Aa	nc	nc	nc	nc	nc	nc	3	nc	2	1	nc	50	nc	nc	nc	3	1	0	0	0	91	69	85
DJ147.43a	nc	nc	nc	nc	nc	nc	nc	0	nc	nc	2	nc	nc	nc	nc	nc	nc	nc	nc	nc	nc	78	nc
DJ147.44a	nc	nc	0	3	3	6	3	1	2	2	2	62	73	6	nc	3	1	0	0	0	89	67	94
DJ147.45a	nc	nc	nc	nc	nc	8	4	0	nc	1	nc	nc	46	nc	nc	1	0	0	0	0	85	98	86
DJ147.46a	nc	nc	0	3	3	1	1	0	4	2	2	61	68	6	0	3	1	0	1	0	89	88	79
DJ147.48a	nc	nc	nc	nc	nc	4	nc	1	nc	2	1	66	63	1	0	3	0	0	1	nc	77	64	84
DJ147.49Aa&Ba	nc	nc	nc	3	nc	9	2	1	8	4	1	48	48	nc	1	1	0	0	0	0	85	67	79
DJ147.51a	nc	nc	nc	nc	nc	nc	3	nc	1	1	1	26	42	6	1	4	1	0	1	0	84	68	56
DJ147.52a	nc	nc	nc	nc	nc	2	1	0	nc	1	1	63	50	4	nc	3	0	0	1	0	87	75	78
DJ147.53a	1	nc	nc	nc	nc	4	2	0	8	2	1	63	39	2	1	3	0	0	1	0	97	73	104
DJ147.55Aa&Ba	nc	nc	nc	nc	1	nc	4	nc	2	2	1	68	nc	6	1	3	1	1	1	0	83	84	75
DJ147.56a	nc	nc	nc	nc	nc	1	1	0	4	3	2	86	74	4	nc	3	1	0	1	0	88	96	85
DJ147.59a	nc	nc	nc	nc	nc	nc	nc	nc	nc	1	1	56	66	6	0	4	0	0	1	0	70	51	83
DJ147.60a	nc	nc	nc	nc	1	nc	1	nc	nc	nc	2	67	nc	nc	nc	3	1	0	0	0	105	73	nc
DJ147.60b	nc	nc	nc	nc	nc	nc	1	nc	nc	2	1	49	nc	6	1	3	0	0	1	0	93	67	72
DJ451.7a	nc	nc	nc	nc	nc	nc	nc	nc	5	3	1	35	35	2	0	3	1	0	1	0	76	94	100
DJ452.2a	nc	0	nc	nc	nc	3	1	1	nc	1	1	11	8	1	0	2	1	0	0	0	70	111	141

Table A3-2 Score sheet Santa Marta Formation flora

'nc' - no comparison

M	Hidden Lake Formation (sq.mm)	Size Class (CLAMP)	Santa Marta Formation (sq.mm)	Size Class (CLAMP)
1	435-1231	micro II	559-1557	micro II - III
2	528-10883	micro II - meso III	193-7189	micro I – meso II
3	208-627	micro I - II	310-1161	micro I - II
4	3523-3736	meso I	185-1962	micro I – micro III
5	767	micro II	260-1221	micro I - II
5B	603	micro II	445-2395	micro II - III
6	59-1122	lepto II - micro II	54-855	lepto II – micro II
7	383	micro I	551-2642	micro II - III
8	113-1635	micro I - III	483-753	micro II
9	130	micro I	-	-
10	852-2317	micro II - III	124-844	micro I - II
11	264-1005	micro I - II	375-827	micro I - II
12	378-4327	micro I – meso I	256-1472	micro I - III
13	204	micro I	70-482	lepto II – micro II
14	131-793	micro I – II	1094	micro II
15	387	micro I	-	-
16	-	-	1521	micro III
17	799	micro II	-	-
18	265	micro I	429-832	micro II
19	-	-	569-2763	micro II - III
20	230-362	micro I	561	micro II
21	571	micro II	1550	micro III
22	-	-	1237	micro II
23	1304	micro II	184-1379	micro I - II
24	-	-	25-1139	lepto II - micro II
25	346-1753	micro I - III	-	-
26	-	-	1791-2685	micro III
27	-	-	266-323	micro I
28	727	micro II	154	micro I
29	-	-	236-283	micro I
30	-	-	357-433	micro I - II
31	365	micro I	1108	micro II
32	972	micro II	-	-
33	-	-	395-504	micro II
34	119	micro I	-	-
35	912	micro II	-	-
36	352	micro I	-	-
37	-	-	839	micro II
38	96	micro I	-	-
39	137	micro I	-	-
40	-	-	528	micro II

Table A4-1 Morphotype size ranges classified according to CLAMP (Wolfe 1993) (see Table 6.13).

Morphotype	Apex	Hidden Lake Formation	Santa Marta Formation
1	<u>acute</u>-attenuate	▣	▣
2	attenuate	▣	▣
3	acute	▣	▣
4	attenuate	▣	▣
5	attenuate	▣	▣
5B	attenuate	▣	▣
6	-	?	▣
7	emarginate	▣	▣
8	-	▣	▣
9	-	▣	-
10	attenuate	▣	▣
11	attenuate	▣	▣
12	acute	▣	▣
13	attenuate	▣	▣
14	attenuate	▣	▣
15	-	▣	-
16	-	-	▣
17	acute	▣	-
18	-	▣	▣
19	? rounded	-	▣
20	acute	▣	▣
21	acute	▣	▣
22	acute	-	▣
23	-	▣	▣
24	-	-	▣
25	rounded	▣	-
26	-	-	▣
27	-	-	▣
28	-	▣	▣
29	rounded	-	▣
30	-	-	▣
31	-	?	?
32	-	▣	-
33	acute	-	▣
34	attenuate	▣	-
35	attenuate	▣	-
36	-	▣	-
37	-	-	▣
38	-	▣	-
39	acute	▣	-
40	-	-	?

▣=present

Table A4-2 Morphotype apices classified according to CLAMP (Wolfe 1993).

Morphotype	Base	Hidden Lake Formation	Santa Marta Formation
1	acute	▣	▣
2	cordate	▣	▣
3	acute	▣	▣
4	acute	▣	▣
5	acute	▣	▣
5B	acute	▣	▣
6	acute	▣	▣
7	-	▣	▣
8	acute	▣	▣
9	rounded	▣	-
10	acute	▣	▣
11	acute	▣	▣
12	acute	▣	▣
13	? acute	▣	▣
14	rounded	▣	▣
15	acute	▣	-
16	-	-	▣
17	-	▣	-
18	acute	▣	▣
19	rounded	-	▣
20	cordate	▣	▣
21	-	▣	▣
22	-	-	▣
23	acute	▣	▣
24	acute	-	▣
25	rounded	▣	-
26	acute	-	▣
27	acute	-	▣
28	-	▣	▣
29	acute	-	▣
30	acute	-	▣
31	acute	▣	▣
32	acute	▣	-
33	-	-	▣
34	rounded	▣	-
35	acute	▣	-
36	acute	▣	-
37	rounded	-	▣
38	-	▣	-
39	-	▣	-
40	cordate	-	▣

▣=present

Table A4-3 Morphotype bases classified according to CLAMP (Wolfe 1993).

Morphotype	Length/width ratio	Hidden Lake Formation	Santa Marta Formation
1	2.59	◙	◙
2	1.98	◙	◙
3	1.91		◙
4	3.27	◙	◙
5	2.71	◙	◙
5B	2.61	◙	◙
6	2.65	◙	◙
7	2.11	◙	◙
8	1.16	◙	◙
9	0.84 min.	◙	-
10	2.87	◙	◙
11	3.23	◙	◙
12	1.49	◙	◙
13	2.02	◙	◙
14	1.42	◙	◙
15	1.98 min.	◙	-
16	-	-	◙
17	?1.9	◙	-
18	2.28	◙	◙
19	1.37	-	◙
20	?1.22	◙	◙
21	2.1	◙	◙
22	2.27 min.	-	◙
23	1.26	◙	◙
24	1.04 min.	-	◙
25	1.66	◙	-
26	2.38	-	◙
27	2.87	-	◙
28	?2.5	◙	◙
29	1.66	-	◙
30	1.69	-	◙
31	0.75	◙	◙
32	-	◙	-
33	?2	-	◙
34	2.66	◙	-
35	1.98	◙	◙
36	2.06 min.	◙	-
37	-	-	◙
38	-	◙	-
39	-	◙	-
40	-	-	◙

◙=present

Table A4-4 Morphotype length/width ratios.

Genus	Author
Aculea	Douglas 1973
Alamatus	Douglas 1973
Anacolosidites	Cookson et Pike ex Potonié 1960
Araliaephyllum	Fontaine 1889
Austrodiospyros	Basinger et Christophel 1985
Brachyphyllum	Brongniart 1828
Cinnamomoides	Seward 1925
Cladophlebis	Brongniart 1849
Classopollis	Pflug 1953
Clavatipollenites	Couper 1958
Coniopteris	Brongniart 1849
Dicotylophyllum	Saporta
Dictyozamites	Oldham
Elatocladus	Halle 1913
Ficophyllum	Fontaine 1889
Gnafalea	Cantrill 1996
Hausmannia	Dunker 1846
Hydrocotylophyllum	Teixeira 1947
Laurelites	Nishida, Nishida et Nasa 1988
Lauriphyllum	Nathorst 1888
Laurophyllum	Goeppert 1853
Leguminosites	Bowerbank 1840
Magnoliidaephyllum	Zastawniak 1994
Monimiophyllum	Zastawniak 1989
Myrciophyllum	Zastawniak 1994
Nothofagidites	Erdtman 1947 ex Potonié 1960
Otozamites	Braun
Pachypteris	Brongniart
Pentaneurum	Li 1994
Protophyllum	Lesquereux
Pterophyllum	Brongniart
Ptilophyllum	Morris
Rhoophyllum	Dusén 1899
Sagenopteris	Presl 1838
Stenopteris	Saporta 1872
Taeniopteris	Brongniart 1828
Timothyia	Cantrill 1996
Williamsoniella	Thomas 1915

Table A5-1 List of authors of fossil genera mentioned in this thesis.

Species	Author
Anona infestans	Berry 1938
Araliaephyllum obtusilobum	Fontaine
Araliaphyllum quinquelobatus	Cantrill 1996
Austrodiospyros cryptostoma	Basinger et Christophel 1985
Berberis corymbosifolia	Berry 1938
Caldcluvia mirabilis	Dusén 1908
Celtis ameghinoi	Berry 1925
Dicotylophyllum elegans	Li 1994
Dicotylophyllum latitrilobatum	Zastawniak 1989
Dicotylophyllum lobatus	Cantrill 1996
Drimys antarctica	Dusén 1908
Drimys patagonica	Berry 1938
Fagus obscura	Dusén 1908
Ficophyllum palustris	Cantrill 1996
Gnafalea binatus	Cantrill 1996
Gnafalea jeffersonii	Cantrill 1996
Hydrocotylophyllum alexandri	Cantrill 1996
Laurelia guiñazui	Berry 1935
Laurelia insularis	Dusén 1908
Laurelites jamesrossii	Poole et Francis 1999
Lauriphyllum nordenskjöldii	Dusén 1908
Laurophyllum conspicuum	Hill 1986
Lomatia mirabilis	(Dusén) Li 1994
Magnoliidaephyllum birkenmajeri	Zastawniak 1994
Monimiophyllum antarcticum	Zastawniak 1989
Myrciophyllum santacruzensis	(Berry) Zastawniak 1994
Myristica fossilis	Engelhardt 1891
Nectandra prolifica	Berry 1938
Nothofagus cretacea	Zastawniak 1994
Nothofagus oligophlebia	Li 1994
Nothofagus serrulata	Dusén 1899
Nothofagus subferruginea	(Dusén) Tanai 1986
Nothofagus ulmifolia	Ettingshausen 1887
Nothofagus variabilis	Dusén 1899
Pentaneurum dusenii	(Zastawniak) Li 1994
Sterculia patagonica	Berry 1925
Sterculia sehuensis	Berry 1937
Sterculia washburnii	Berry 1928
Tetracera patagonica	Berry 1925
Timothyia trinervis	Cantrill 1996

Table A5-2 List of authors of fossil species mentioned in this thesis.