VARIATION IN THE NATIVE WOODLAND COVER OF THE MORAR BASIN, WITH PARTICULAR REFERENCE TO THE PALAEOLIMNOLOGY AND PALAEOMAGNETIC RECORD FROM LOCH MORAR, HIGHLAND REGION, SCOTLAND

- by -

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ABSTRACT

This thesis examines aspects of the palaeolimnological and palaeomagnetic records from Loch Morar, Highland Region, Scotland. The palaeoecological interpretation of these records is augmented by a review of the floristic character of the current vegetation.

Palaeomagnetic data from a long core display secular variations of declination and inclination for an unknown time interval. The top metre has been compared with records from northwest Europe covering the last 10,000 years and has been tentatively assigned to that time interval. A preliminary pollen analysis appears to confirm this interpretation. Stabilization of terrain is indicated by declining magnetic susceptibility, coupled with constant sediment accumulation rates during the period represented by the top metre of the sediment core.

The fossil diatom record from the same provides an insight into the tophic status of the lake and catchment areas, suggesting significant acidification during the Holocene Period. Iron Oxide deposition suggests a widespread development of waterlogged soils during the same period.

A qualitative examination of woodland sites within the catchment area indicates that relict native oak (*Quercus petraea* x *robur*) and birch (*Betula pubescens* ssp. *odorata*) woodland, referable to the *Betuletum Oxaleto-Vaccinetum* and *Betula*-herb noda, survives at several sites around Loch Morar, and that native Scots pine (*Pinus sylvestris* var. *scotica*) woodland, referable to a combination of the *Pinetum Hylocomieto-Vaccinetum* and *Pinetum Vaccineto-Callunetum* association, occurs on an archipelago in the loch. The presence of *Pinus sylvestris* var. *scotica* at this site suggests that the geographical distribution range of this taxon extends farther westwards in mainland Scotland than previously recorded.

A phytosociological study of the epiphytic (corticolous) lichen flora previously record from these woodland sites by Dr Francis Rose, and the application of the Revised Index of Ecological Continuity *sensu* Rose (1976) indicates that they have experienced ecological continuity of high tree cover, as opposed to coppice, over a long period.

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PREFACE

This thesis examines the history of native woodland in the Morar Basin, in the Highland region of Scotland, including evidence in palaeolimnological and palaeomagnetic records from Loch Morar. The Morar Basin lies within an area of outstanding natural beauty and scientific interest, in a remote region of the Western Highlands of Scotland. A prominent topographic feature of this area is Loch Morar, which is noteworthy as Britain's deepest freshwater basin.

The mountain slopes and hill-sides surrounding the loch support broad-leaved deciduous woodland cover, which occurs as discontinuous fragments of varying extent, while an archipelago of small islands situated near the western end of Loch Morar supports stands of coniferous woodland.

The Morar Basin was initially investigated between 1897 and 1909, as part of a bathymetrical survey of the 542 principal freshwater basins in Scotland, which was directed by Sir John Murray and Lawrence Pullar, following successful oceanographic expeditions undertaken on board HMS Challenger *circa* 1873 (Murray and Pullar, 1910).

Almost one hundred years later, interest in the limnology of Britain's deepest basin resumed with the Loch Morar Survey (1970-1972) which was followed by the Loch Morar Expeditions (1973-1977) and later by the Loch Ness and Morar Project, which were directed by Adrian Shine Esq. and supported in their scientific objectives by the Royal Geographical Society, London. The author participated in several volunteer expeditions with the Loch Ness and Morar Project (Shine and Martin, 1988), whilst an undergraduate student at the University of London.

The thesis extends the scope of earlier investigations by examining the status of the surviving fragments of woodland vegetation within the Morar Basin, with the particular aim of elucidating whether the stands of trees in this area represent relics of former climax forest. Furthermore, the floristic composition and structure of these scarce fragments of woodland raised significant ecological questions, which the thesis examines in an analysis of sediments collected from the deep water zone of Loch Morar.

The thesis is comprised of six chapters. The regional environment is described in Chapters 1 and 2, which cover aspects of geology and topography, including the origin and lithology of the ancient bedrock; geomorphological features, including the margin of the last glacier (Loch Lomond Stadial) ice which occupied Loch Morar; present climatic conditions and soil types which occur in the catchment area.

The status of the surviving woodland is examined in Chapters 3 and 4, which include aspects of the geographical distribution, floristic composition and phytosociology of native Highland woodland, with particular emphasis upon the post-glacial continuity of the woodland cover surrounding Loch Morar. Available information regarding the ecology and phytosociology of epiphytic (corticolous) lichens which occur in western Scotland is reviewed in Chapter 4, with a description of lichenological indicators of age and environmental continuity in British woodlands. Data from field record cards relating to British Lichen Society lichen surveys of woodland vegetation within the Morar Basin were collated and analysed by the author in terms of the phytosociology of the lichen communities, along with an assessment of the lichenological indicators of ecological continuity of high tree cover. The results of these analyses are presented in Chapter 4.

The post-glacial (Holocene) history of the Morar Basin is explored in Chapter 5 which describes sedimentary evidence from Loch Morar and a nearby hill-lochan. The palaeomagnetic record obtained from long sediment cores collected from Loch Morar is presented as the principal method of dating the record of palaeoenvironmental change. An outline analysis of fossil pollen preserved in one sediment core from the loch, which was kindly supplied to the author, is also presented. Unfortunately, the scope of this analysis is limited. Nevertheless, it provides supplementary data relating to the history of the tree cover, and also provided independent chronological verification of the palaeomagnetic record obtained from Loch Morar.

The palaeolimnology of the Morar Basin and its possible implications for the status of former vegetation and soil conditions within the catchment area are indicated by reference to the analysis of the fossil diatom record, including the variation in acidophilous taxa, and to the incidence of Iron Oxides preserved in the sedimentary succession from Loch Morar.

A brief commentary is also included on the archaeological background of this region, along with an assessment of possible factors which may have been implicated in the history of the surviving native woodland cover of the Morar Basin.

A summary of the principal findings is presented in Chapter 6. A correlation of the lithostratigraphy, chronostratigraphy and biostratigraphy of the sedimentary succession in the profundal zone of Loch Morar is presented in tabular form at the end of Chapter 6.

Plant nomenclature follows Clapham, Tutin and Warburg (1962, 1987), Watson (1968) and Hawksworth, James and Coppins (1980) for vascular plants, mosses liverworts and lichens respectively. Diatom nomenclature is indicated separately in Chapter 5. Place names are spelled according to the Ordnance Survey (1:50,000 scale) Landranger Series and Second Series (1:25,000 scale) maps.

CHAPTER ONE

ASPECTS OF THE GEOLOGY OF THE MORAR BASIN

> "The mingling of mouldering knolls with rough angular rocks, the vertical rifts (*sic*) that gape on the face of crag and cliff ..... the strange twisted crumpled lines of stratification, the blending of white bands of quartz with dark streaks of hornblende that vary the prevailing grey or brown or pine hue of the stone, the silvery sheen of the mica and the glance of the feldspar or the garnets, the crusts of grey and yellow lichen or the green-velvet-like moss ..... these are features which we recognise at once as distinctly and characteristically Highland" (A. Giekie, 1865).

GEOGRAPHICAL LOCATION

The Morar Basin is located in the western part of Lochaber District, in the Highland Region of Scotland, between latitude 56°30'N and 57°00'N, and longitude 5°20'W and 6°00'W. The geographical location of the Morar Basin is indicated in Figure 1. The area derives its name from the Gaelic *Mordhobar* (large water) and probably refers to the magnificent freshwater loch called Loch Morar, which forms a principal topographic feature in the landscape (Macdonald, 1888). A view of Loch Morar looking due eastwards along its principal axis is illustrated in Plate 1.

The Morar district comprises a western sea-board, which is separated from the islands of the Inner Hebrides (Western Isles) by a maritime strait called the Sound of Sleat. The eastern part of the Morar district comprises hills and a number of closely spaced mountain summits of Lochaber District, which form part of the principal watershed of the Scottish Highlands. To the north are two principal sea-lochs, called Loch Nevis and Loch Hourn, in Knoydart District. To the south, is Moidart District and Ardnamurchan, the westernmost peninsular of the Scottish mainland. From the low hills of Morvern in the south, the mountains gradually increase in elevation northwards to exceed 914 metres OD (ordnance datum) around Loch Hourn.

The districts of Knoydart, Morar, Moidart and Ardnamurchan comprise the Rough Bounds - derived from the Gaelic *na Garbh Cruachan*. This region was appropriately described by Adamnan (*circa* 685 AD), Saint Columba's biographer, as *aspera et saxosa* - rough and stony (Lacaille, 1951). An outstanding feature of the topographic relief is the highly indented sea-board, with long sea-lochs penetrating far into the mountainous tracts; the summits in Knoydart, Morar and Moidart provide a spectacular vista seaward across the Hebrides. The bedrock of this western sea-board comprises predominantly metamorphic Moine schist rock.

The greater part of the land in the Rough Bounds is currently utilized for livestock grazing, by sheep and deer, with forestry in the glens, and fishing in the lochs. The terminus of the West Highland Railway is located at the port of Mallaig.

GEOLOGY OF THE CALEDONIAN MOUNTAINS IN NORTHWEST SCOTLAND

The rock formations of the British geological succession generally exhibit progressively older formations in a northwesterly trend across the British Isles. Indeed, the rock formations of northern Scotland include the oldest series of the geological succession, namely the Lewisian, Moinian and Torridonian, which are

Fig.1 THE GEOGRAPHICAL LOCATION OF THE MORAR BASIN

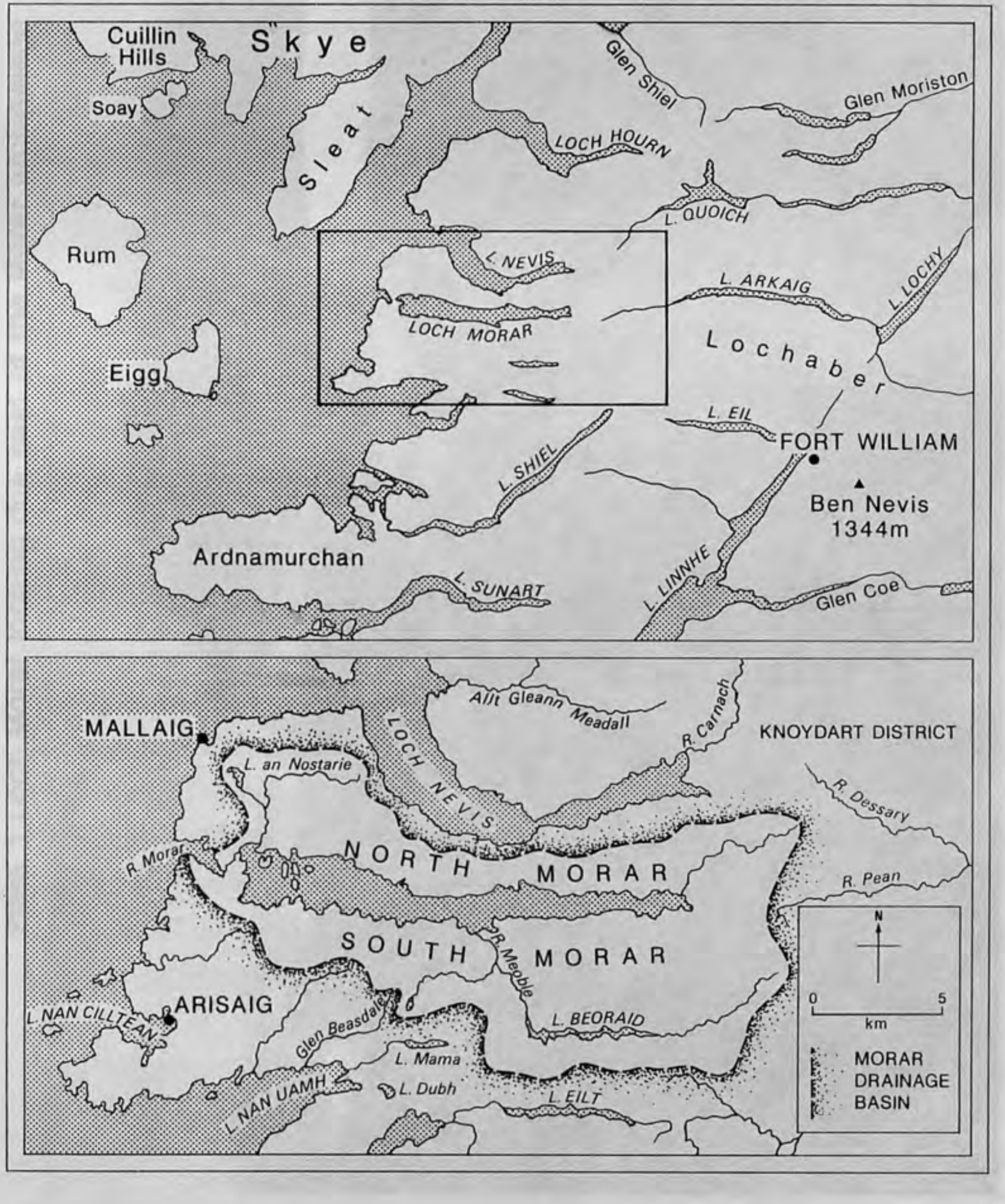
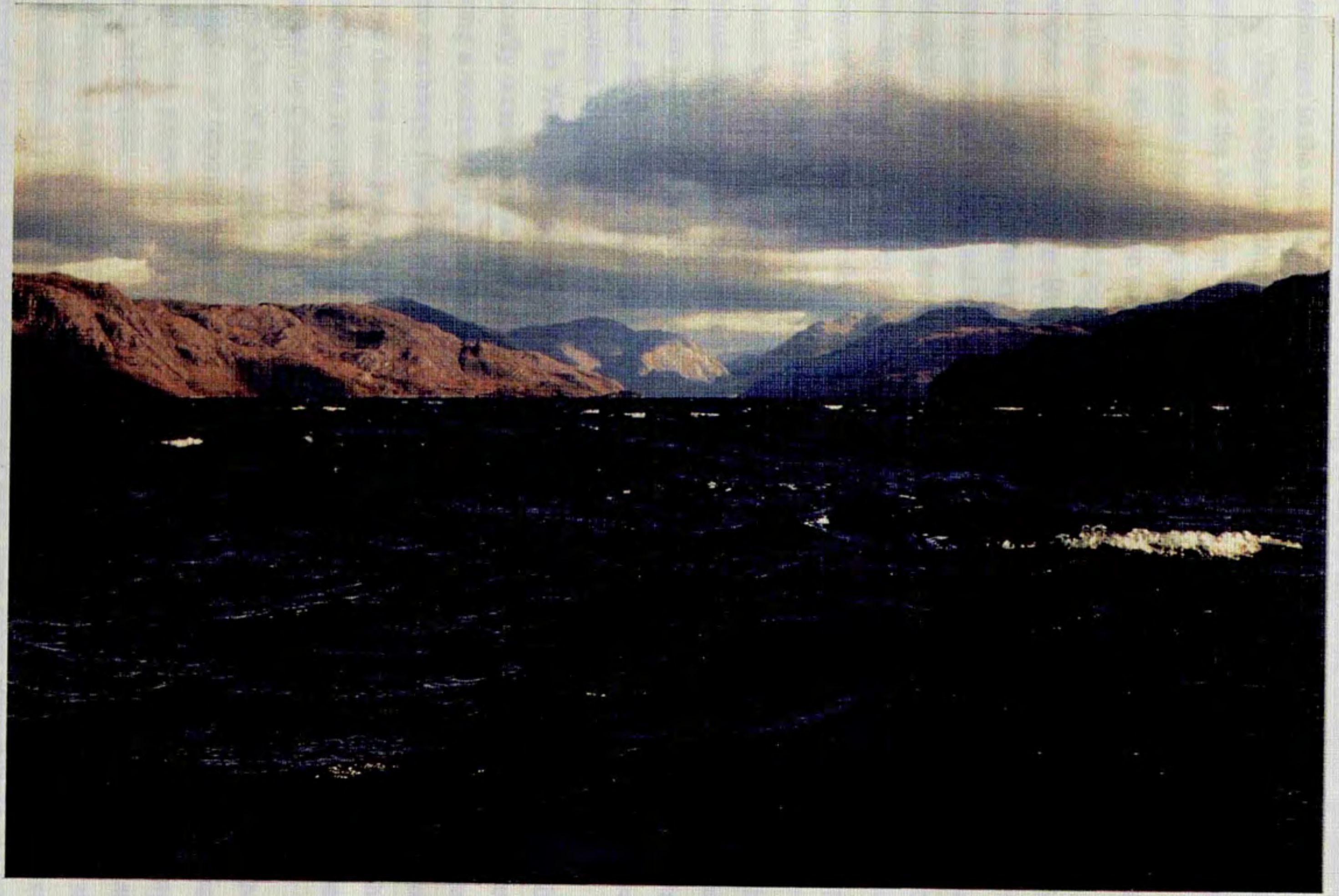


Plate 1 Loch Morar looking due east of the Morar archipelago



Pre-Cambrian and Archaean in age, i.e. pre-600 million years BP. These rock formations have contributed to the rugged landforms of a country which lies within the tract known as the Highlands of Scotland.

The geology of the Scottish Highlands is remarkable for the antiquity of the rock succession, while also exhibiting some of the most complex geological structures in the world, e.g. the Moine thrust-plane.

The following chapter outlines some of the most important aspects of the geology of the Northern Highlands of Scotland, with particular reference to the northwestern mountains, and the sea-board of the Morar district.

A striking feature of the Scottish rock formations is the clearly defined northeast to southwest alignment of the geological succession. This trend is evident throughout the British Isles, particularly in Scotland, where it is so pronounced that it forms a principal and dominant feature in the folds and faults of the mountains. This trend is interpreted as having arisen during a former period of mountain building, when the existing sedimentary rocks were folded and subsequently uplifted to form high ranges of fold mountains. The dominant structural alignment of the Scottish Highlands, which is termed the Caledonian trend, is attributed to a period of mountain building - the Caledonian orogeny - which occurred between approximately 470 and 400 million years ago. The Caledonian trend is responsible for the characteristic northeast to southwest "grain" of many of the Scottish landforms; the mountain tracts of the western coastal sea-board in the Morar area clearly reveal a north-northeast to south-southwest structural alignment.

In Western Europe, the remanents of the Caledonian diastrophism, which broadly corresponds with the Late Silurian-Early Devonian periods, may be traced along a northeast to southwest alignment from Scandinavia, through Scotland and into northwest Ireland. Indeed, the elevation of Caledonian mountain range which arose during this period is considered to have exceeded the present height of the Himalayan mountains. The denuded relics of the Caledonian orogeny, which are termed the Caledonides, now form the principal lineaments of highland Britain.

One of the principal rocks which occur in the Scottish Highlands is the complex of Moinian rocks, comprising a sequence of mica schists and feldspar granulites, altered by high-grade regional metamorphism both prior to and during the Caledonian orogeny. The Moinian rocks are metamorphic and derive from sedimentary rocks which experienced prolonged pressure from compressive forces exerted during periods of mountain building. Furthermore, these rocks were also affected by contact metamorphism, arising from their close proximity to molten magma originating from deep sources in the earth, and by metasomatic metamorphism arising from the infiltration of chemically active fluids.

The isotopic composition of rock associated with the Scottish Moinian formations indicates that a period of sedimentation of predominantly fine-grain size clastic material and the formation of sandstone, marked the early development of the Moinian rocks at between 1,200 million and 1,000 million years BP. These sedimentary rocks were subsequently affected by metamorphic processes, possibly associated with a Pre-Cambrian episode of mountain building dated at *circa* 1,000 million years BP (*personal communication*, Dr David Powell, University of London, 1989).

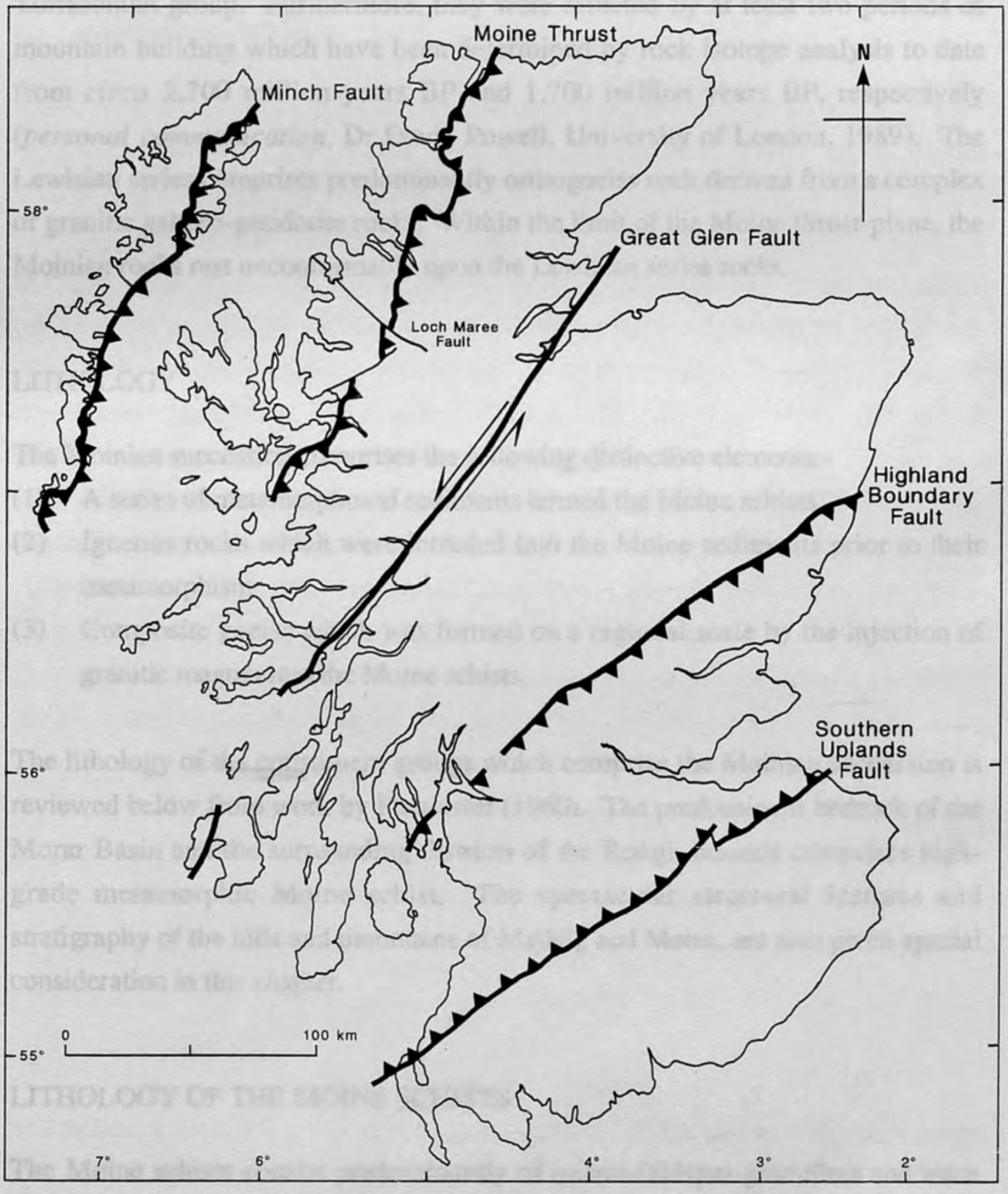
The character of the constitutent minerals and clastic material of the sedimentary formations was radically altered as a result of these metamorphic processes, thus, the fine grain argillaceous sedimentary rocks, e.g. clays, were converted into pelitic Moine schists, while the arenaceous sedimentary rocks, i.e. sandstones, were converted into psammitic Moine schists. Furthermore, the Moinian rocks also developed a characteristic schistosity which is one of the most distinctive textural features arising from the metamorphism of fine-grain sediments, i.e. a marked segregation of minerals into thin layers, together with a re-orientation of plate-like minerals including mica, resulted in the formation of highly distinctive cleavage planes or schistosity in the Moinian rock.

The Moine schist rock of the Northern Highlands was subsequently profoundly affected during the Caledonian orogeny, dated at between *circa* 470 and 400 million years BP. The Moinian rock was subjected to high-grade regional metamorphism, which resulted in the formation of a highly folded and faulted complex of predominantly micaceous schists and quartz-feldspar granulites.

The Moinian group of rocks occurs throughout most of the Northern Highlands of Scotland and outcrops over an area of approximately 9,065 square kilometres (3,500 square miles) extending from the Great Glen (Glen Mor) fault northwestward to a complex tectonic feature known as the Moine thrust-plane, which extends irregularly for a distance of approximately 320 kilometres from the Sound of Sleat, due west of the Morar sea-board, to Whetter Head on the north coast of Scotland. In addition, the Moinian rocks also crop out south of the Great Glen fault, in the northeastern part of the Grampian Mountains. The principal geological faults in Scotland are indicated in Figure 2.

During the Caledonian orogeny, prolonged deformation and folding resulted in the northwestward movement of the Moinian rocks across the underlying Cambrian and Pre-Cambrian rocks. The western limit of the Caledonian trend in the Scottish Highlands occurred along the complex Moine thrust-plane. Westward of this feature, the remainder of the Scottish mainland, along with the Outer Hebrides and most of the Inner Hebrides (with the exception of the Island of Mull and part of the Isle of Skye, which lay within the western limit) were generally

Fig.2 PRINCIPAL GEOLOGICAL FAULTS IN SCOTLAND



Source: Oxford Atlas (O.U.P.)

unaffected by the events of the Caledonian orogeny. This region of Scotland is often referred to as the Archaean foreland.

The rocks of the Archaean foreland comprise predominantly Lewisian gneiss and Torridonian sandstone. In the geological succession, the Torridonian rocks rest unconformably on rocks of the Stoer Group which may be contemporaneous with part of the Moinian succession, however, further data are required to establish this point. The Lewisian series of rocks are considerably older than the Torridonian group. Furthermore, they were affected by at least two periods of mountain building which have been determined by rock isotope analysis to date from *circa* 2,700 million years BP and 1,700 million years BP, respectively (*personal communication,* Dr David Powell, University of London, 1989). The Lewisian series comprises predominantly orthogneiss rock derived from a complex of granitic gabbro-peridotite rocks. Within the limit of the Moine thrust-plane, the Moinian rocks rest unconformably upon the Lewisian series rocks.

LITHOLOGY

The Moinian succession comprises the following distinctive elements:-

(1) A series of metamorphosed sediments termed the Moine schists

(2) Igneous rocks which were intruded into the Moine sediments prior to their metamorphism

(3) Composite gneiss which was formed on a regional scale by the injection of granitic magma into the Moine schists.

The lithology of the constituent groups which comprise the Moinian succession is reviewed below from work by Phemister (1960). The predominant bedrock of the Morar Basin and the surrounding districts of the Rough Bounds comprises high-grade metamorphic Moine schist. The spectacular structural features and stratigraphy of the hills and mountains of Mallaig and Morar, are also given special consideration in this chapter.

LITHOLOGY OF THE MOINE SCHISTS

The Moine schists consist predominantly of quartz-feldspar granulites and mica schists, along with subordinate members which include calcite-silicate granulites and very rarely, crystalline limestones. Muscovite is also characteristic of the Moinian rocks, while in contrast, it is rare in acid Lewisian rocks. Throughout its entire range this series presents a banded aspect where it crops out, with alternate layers of quartz-feldspar layers and predominantly micaceous layers. This characteristic small-scale banding reflects, in miniature, the composition of the series, with alternating psammitic, pelitic, and semi-pelitic groups.

The lithology of the three groups which comprise the Moine schists, namely psammitic, pelitic, and semi-pelitic schists, respectively, are briefly described below.

(1) PSAMMITIC SCHISTS

These vary from quartzose schists, and occasionally quartize, to massive grey quartz feldspar granulites, which contain biotite and muscovite. Biotite is not common in the quartzose schists and quartzites. The quartz and feldspar are not segregated into thin laminae, consequently the less micaceous varieties tend to be massive. The micaceous schists usually exhibit good parallel-plane schistosity owing to the disposition of mica in parallel orientations. The feldspar is typically either orthoclase or oligoclase. The quartz-feldspar granulites have a sparkling and crystalline appearance, often with conspicuously larger grains of quartz and feldspar.

Layers of heavy minerals are also common among the granulite schists, and in some cases form bands up to 10 millimetres in thickness. These minerals include garnet, which is a common although inconspicuous constituent, along with epidote, apatite, zircon, sphene, orthite and iron ores. Ilmenite and magnetite are also frequent additions. These minerals often exhibit a rounded form, even though the associated quartz and feldspar are entirely granular. Adjacent layers often show concentrations of a particular mineral. Thus, in Moidart district, where such bands are conspicuous in the schists, some layers are entirely composed of sphene and magnetite. Thin bands and lenses of haematized magnetite, together with quartz, feldspar, muscovite and epidote are exposed in schists at Creag Iasgach, near Mallaig.

(2) PELITIC SCHISTS

The pelitic schists consist predominantly of deep brown biotite with muscovite. The schists are either black or silver in colour, according to the proportions of biotite or muscovite, which are present. They contain a variable proportion of quartz and plagioclase feldspar. These minerals are often aggregated into lenticular laminae. Schistosity is well developed and may be either plane or wavy. Garnets are common in the mica schist, often occurring as crystals exceeding 25 millimetres diameter.

Staurolite mica schists occur rarely in pelitic belts, while kyanite is extremely rare. Sillimanite-bearing pelitic schists have been recorded on Beinn Gaive in Moidart district, however, this mineral is uncommon in the Moine schists, except where it is associated with granitic injection complexes.

Pelite is unique in the Moine stratigraphic succession, because it contains thin bands and lenticels of calcite-silicate rock metamorphosed from marl sediments.

(3) SEMI-PELITIC SCHISTS

The semi-pelitic schists are often dark grey and contain variable proportions of biotite. They generally exhibit well developed parallel-plane laminae. In a common variety known as "pepper and salt" Moine schist, the mica is distributed in a uniform and poorly orientated manner. These schists exhibit a speckled appearance in many cases, and tend to be massive.

A complete gradation in lithology exists in the Moine series. Thus, mica schist and siliceous granulite represent two opposite extremes of a continuous series, while the semi-pelitic schists represent intermediate members of this series.

(4) MINOR MEMBERS OF THE MOINE SCHISTS

Zoisite granulites comprise the most important subordinate components of the Moine schists. They are usually interbanded as laminae, which are less than 30 centimetres thick, within semi-pelitic schists, as white or dark grey compact rocks speckled with red garnet and dark green hornblende. They are frequently banded as a result of the parallel disposition of garnetiferous, hornblendic and biotite layers; other constitutents include quartz and oligoclase feldspar. Bands of epidote and epidosites, which contain pyroxene or amphibole also occur among the pelitic schists, while thin bands of calcite-garnet granulite commonly occur among the quartz-feldspar granulites.

(5) HORNBLENDIC GNEISSES

The hornblende-gneisse rocks of the Morar district comprise banded, striped and massive gneisses of ultrabasic, basic and acid types which are locally rich in garnet and often associated with biotite and bands of epidote. Hornblende-gneiss rocks are typically interbanded with sedimentary granulites and schists which correlate with the lithostratigraphic succession of the Moinian rocks (Richey and Kennedy, 1939). These rocks have been interpreted as representing thrust-masses of Lewisian age. Indeed, hornblende is particularly characteristic of the Lewisian series (Kennedy, 1955; Lambert, 1958, 1959a, 1959b). However, no evidence of unconformity between the gneisses and the contiguous granulites has been recorded to date. Significantly, marginal interbanding is a common feature. Narrow bands of Moine granulite schist occur within broad outcrops of hornblende-gneiss, while bands and thin layers of hornblende-gneiss correspondingly occur within the granulite. Minor basic and ultrabasic pre-foliation intrusions are numerous within the belts of hornblende-gneisses, while to a lesser extent they also occur within the adjacent Moine schist granulites. The gneisses and granulites also exhibit the same dip and strike, and share a common folding. Thus, the belts of hornblende-gneiss may be regarded as part of the Moinian rocks (Phemister, 1960).

STRATIGRAPHY AND STRUCTURE OF THE MOINIAN ROCKS IN THE MALLAIG-MORAR-ARISAIG AREA

A local stratigraphical succession, based upon evidence of current bedding, was initially formulated for Arisaig and Morar by Richey and Kennedy (1939), who demonstrated the existence of a great fold, termed the Morar Anticline, which is locally overturned on its western margin, with an axial trend orientated approximately north-south in direction from Loch Nevis to the Sound of Arisaig. The sedimentary core-rocks of this area were assigned to the Moinian rocks by MacGregor (1948).

The stratigraphical succession of the Moine and Lewisian rocks for the area around Mallaig is summarized in Table 1. This stratigraphical succession is based upon the work of Richey and Kennedy (1939), Kennedy (1955), Ramsay and Spring (1962) and Lambert and Poole (1964a, 1964b).

Lambert and Poole (1964b) adopted the stratigraphic succession proposed by Ramsay and Spring (1962), and made two minor modifications. Firstly, it was noted that the Number 3 'Pelite' is frequently missing from the succession; secondly, at some localities the 'Basal Pelite' grades downward into a psammite, which is in contact with the Lewisian. Thus, the Number 1 Basal Pelite *sensu* Ramsay and Spring (1962) was sub-divided into a 1A Psammite, and 1B Semi-Pelite, respectively, by Lambert and Poole (1964b).

Table 1 - The stratigraphical succession of the Moinian and Lewisian rocks for the region around Mallaig

Kennedy (1955)		*Ramsay & Spring (1962)*		*Lambert & Poole (1964b)*
Upper Psammitic group	m^{3b} m^{3a}	No.6	Psammite	Ditto
Striped and Pelitic group	m^{2c} m^{2b} m^{2a}	No.5	Pelite and Semi-Pelite [calc-silicate ribs in the upper part and extending into the lowest No.6]	Ditto
Lower Psammitic group	m^{1c} m^{1b} m^{1a}	No.4	Psammite	Ditto
SLIDE				
Pelitic group	m^{2}	No.3	Pelite	No.3 *sensu* Ramsay and Spring (1963) is frequently missing
Lower Psammitic group	m^{1}	No.2 No.1	Psammite Basal Pelite	Ditto In Morar: 1B Semi-Pelite In Morar: 1A Psammite
SLIDE			UNCONFORMITY	
Lewisian	A		Lewisian	

Source: Phemister (1960)

By virtue of the excellent state of preservation of the sedimentary structures in the Moine schists occurring around Morar and Mallaig, it has also proved feasible to estimate the thickness of groups of the Moinian rocks in this area (Kennedy, 1955). Since the width of the outcrops may vary over a geographical area, as a consequence of sliding during the folding process, these estimates are reliable only for specific localities. The three groups of the Moine schist which occur to the west of the core of the Morar anticline have the following estimated magnitudes (Kennedy, 1955):-

(i) The Upper Psammitic group, near Arisaig, is approximately 366 metres thick
(ii) The Striped and Pelitic group, near Mallaig, is approximately 1,067 metres thick
(iii) The Lower Psammitic group, near Mallaig, is approximately 1,067 metres thick

The Moinian rocks present a constant lithological aspect, consisting of interbedded metamorphosed arenaceous and argillaceous rocks; calcareous rocks are rare and conglomerates composed of small pebbles are scarce, while breccias are absent. The group of hornblende-gneiss rocks present an interesting variation within the Moine rocks. Significantly, an interbedding of hornblende-gneiss and siliceous granulite, and the inclusion of disinct igneous rocks, including pure hornblende, along with metamorphosed rocks, including biotite schist with garnets, are characteristic features of the Moine rocks.

The hornblende-gneiss rocks have been interpreted as probably representing interbedded basic tuffs, lava and associated minor intrusions. The narrow banded structure of the gneiss is frequently associated with small basic and ultrabasic intrusions (Peach and Horne, 1884, 1930). Significantly, the para-gneiss of the Lewisian formations exhibit a distinct lithological dissimilarity to the hornblende gneiss of the Moine rocks. The para-gneiss represent metamorphosed arenaceous rocks which are rich in calcareous and carbonaceous constituents.

Chemical analysis of the Moine schists has permitted the following inferences to be made regarding the derivation of the members of the Moine rocks (Phemister, 1960).

Member of the Moine schist rocks	*Probable precursor*
Siliceous granulite	Sandstone, more or less feldspathic
Pelitic schist	Shale
Staurolite-garnet-mica schist	Shale, of a more magnesian type
Zoisite-hornblende granulite	Siliceous marl

Geological surveys of the Morar and Arisaig districts (Richey and Kennedy, 1939) have revealed the existence of unusually well-preserved original sedimentary structures in the Moine schists. These structures include current-bedding, cross-bedding, ripple-marking, slump-folding, contemporaneous shrinkage cracking, contemporaneous erosion, and depositional laminae. The existence of these structures suggests that the Moinian sediments were originally deposited in shallow water.

No evidence of fossils has been found in the Moinian rocks, even in places where the original character of the sediment is sufficiently well-preserved to indicate depositional structures. Fossils are characteristically uncommon in similar types of metamorphic rock of Palaeozoic age.

A stratigraphical discordance, interpreted as an unconformity, exists between the Moinian rocks and inliers of Lewisian orthogneiss and paragneiss. The recognition of this apparent unconformity between the Lewisian and Moine schist rocks, coupled with their lithological dissimiliarity, suggests that the Moine rocks post-date the Lewisian rocks in Scotland (Peach *et al.*, 1907). This view is further supported by recent analysis of the rock isotope composition of the Palaeozoic succession in Scotland (*personal communication,* Dr David Powell, University of London, 1989).

Plate 2 The deepest part of Loch Morar, looking south-east to Druim a'Chuirn, South Morar

CHAPTER TWO

TOPOGRAPHY, CLIMATE AND SOILS OF THE MORAR BASIN

Lengthy periods of denudation have reduced the scale and magnitude of many of the Caledonian mountain ranges during geological history. The effects of repeated glaciation during the Quaternary period (*circa* 2 million years BP to present) have modified the topographic relief of the Highland landscape to a considerable extent. Paradoxically, unconsolidated deposits of the youngest geological period often rest directly upon bedrock which is associated with some of the oldest rock formations in the British geological succession; rocks and sediments representing the intervening geological record have been removed almost entirely from vast areas of the landscape in the Scottish Highlands, as a direct result of erosion by ice-sheets and valley glaciers.

Indeed, erosion by glacier ice has produced an extremely irregular rocky landscape, and a highly indented coastline with fjord-like sea lochs which have a high length to width ratio and steep sides. Many sea lochs have been affected by glacier ice descending to sea-level and far below. Indeed, submarine erosion has created sea floor rock basins to 323 metres depth around the Isle of Skye (Binns *et al.*, 1973) and the adjacent Inner Sound of Raasay, thus forming the deepest area of the sea around the coast of the British Isles (Sissons, 1976); many over-deepened valleys have been flooded in coastal areas to produce spectacular coastal scenery. Farther inland, mountain ranges have been greatly dissected so that deep valleys or glens separate mountain ridges, each of which is divided by cols which are often glacially pronounced into a series of summits and peaks. These Highland glens often retain freshwater lochs within rock basins which have been over-deepened by glacier erosion.

A bathymetrical survey of the principal freshwater lochs in Scotland by Murray and Pullar (1910) revealed that these lochs frequently exhibit a threshold near their entrances, while descending on the landward side to depths which far exceed those in the seaward continuation. Furthermore, these lochs also exhibit many fjord-like characteristics; they are often steep-sided, roughly linear in form, and often descending to great depths. Loch Morar provides a spectacular example of a major rock basin which has been over-deepened by glacier erosion. Indeed, it also represents the deepest lake in the British Isles, with a maximum recorded depth of 310 metres, with the majority of the basin occurring 300 metres below present sea-level (Murray and Pullar, 1910).

A view across the deepest part of Loch Morar, looking south-eastwards to Druim a'Chuirn, South Morar, is illustrated in Plate 2.

Loch Morar is a large freshwater basin which is situated near the western seaboard of Inverness-shire, Highland Region, forming a dominant feature in the topography of the Morar Parish, Lochaber District (National Grid reference NM 780 900).

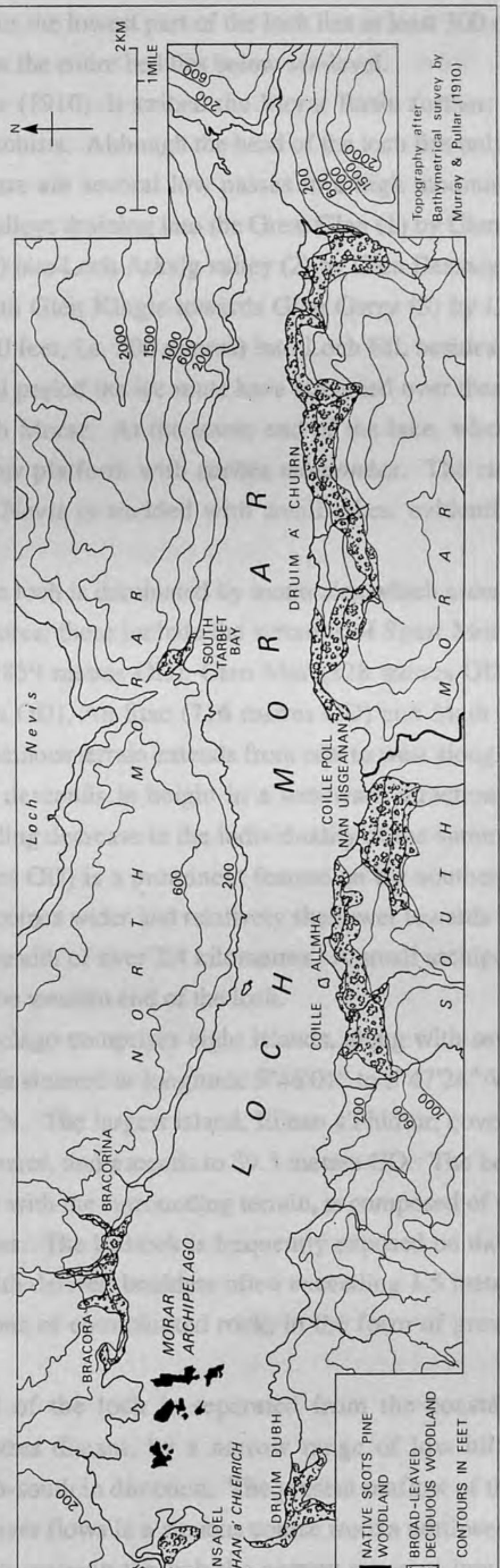
Murray and Pullar (1910) described Loch Morar thus: "This is a large and beautiful loch, lying amid wild and magnificent scenery on the west coast of Inverness-shire, in the southwest portion of that county, immediately to the south of Loch Nevis, which is a sea loch running inland for 12 miles (19.3 kilometres) from the Sound of Sleat. The west end of Loch Morar is about 3 miles (4.8 kilometres) from Arisaig, and 2.5 miles (4.0 kilometres) from Mallaig. Morar station on the Mallaig branch of the West Highland Railway, is within a few hundred yards of the west end .... Loch Morar is the principal loch lying in the basin of the River Morar, and gives great interest to the whole area from the fact that it is not only the deepest lake in Scotland, but in the British Isles.

There are several islands, more or less richly covered with vegetation at the west end of the loch and parts of the surrounding land, especially on the north side are fairly well wooded, all of which greatly adds to the beauty and picturesqueness of thes cenery at this part, but as one proceeds eastwards towards the head of the loch the scenery becomes wilder, the vegetation more scanty, and the mountains on both sides of the loch rise higher and more steeply. At many places on the north shore they rise precipitously from the water's edge, and around the head of the loch they reach a height of fully 3000 feet (914 metres)."

The physical relief and principal areas of native woodland surrounding Loch Morar are illustrated in Figure 3.

Loch Morar lies in a valley which has been subjected to intense erosion by glacier ice during its geological history; it is orientated in a due east-west direction, and irregularly traverses the strike of the Moine bedrock, which is principally directed north-northeast to south-southwest; it is long, at a little over 18.5 kilometres in length; narrow, with a mean breadth of nearly 1.45 kilometres, and deep, with a mean depth of 86.6 metres, and a maximum depth of 310 metres. The maximum depth occurs nearly mid-way between the two ends of the loch. When the loch was surveyed by Murray and Pullar in June 1902, the height of the surface was found to be 9.3 metres above sea-level (determined in relation to the Liverpool

Fig.3 RELIEF AND PRINCIPAL AREAS OF NATIVE WOODLAND IN THE MORAR BASIN



Datum for sea-level), thus the lowest part of the loch lies at least 300 metres below sea-level. Indeed, almost the entire bed lies below sea-level.

Murray and Pullar (1910) described the Morar Basin further: "[A] typical rock basin in granulitic schists. Although the head of the loch lies only a few miles from the watershed, there are several low passes in a high mountainous region connecting it with the valleys draining into the Great Glen (1) by Glen Pean (under 500 feet, i.e. 150 metres) into Loch Arkaig valley (2) by Glen Dessary (under 1000 feet, i.e. 300 metres) into Glen Kingie towards Glen Garry (3) by Loch Beoraid over the col (under 1000 feet, i.e. 300 metres) into Loch Eil, besides other higher gaps. During the glacial period the ice must have streamed over these passes and concentrated upon Loch Morar. At the lower end of the lake, where the valley widens there is a shallow platform with *roches moutonées*. The ridge between Loch Morar and Loch Nevis is studded with small lakes, evidently due to ice erosion."

The east end of the loch is dominated by mountains which ascend steeply on both north and south shores; these include the summits of Sgurr Mor (612 metres OD), Sgurr na h-Ride (859 metres OD), Carn Mor (828 metres OD), Sgurr nan Coireachan (955 metres OD), An Stac (716 metres OD) and Math Bheinn (710 metres OD). The mountainous terrain extends from east to west along both sides of the loch and gradually descends in height in a westward direction towards the coast, with a corresponding decrease in the individuality of the summits, of which Sithean Mor (600 metres OD) is a prominent feature on the southern side of the loch. The basin also becomes wider and relatively shallower towards the west end, attaining a maximum breadth of over 2.4 kilometres. A small archipelago of rock islands is situated near the western end of the loch.

The Morar archipelago comprises eight islands, along with several smaller isles. The archipelago is situated at longitude 5°46'01" to 5°47'24" W by latitude 56°57'20" to 56°57'55" N. The largest island, Eilean a'Phidhir, covers an area of approximately 6.86 hectares, and ascends to 39.3 metres OD. The bedrock of the archipelago, in common with the surrounding terrain, is composed of metamorphic schist of the Moine series. The bedrock is frequently exposed on the islands, and the ground is strewn with derived boulders often exceeding 1.5 metres in height, along with accumulations of comminuted rock, in the form of gravel, sand and finer mineral fractions.

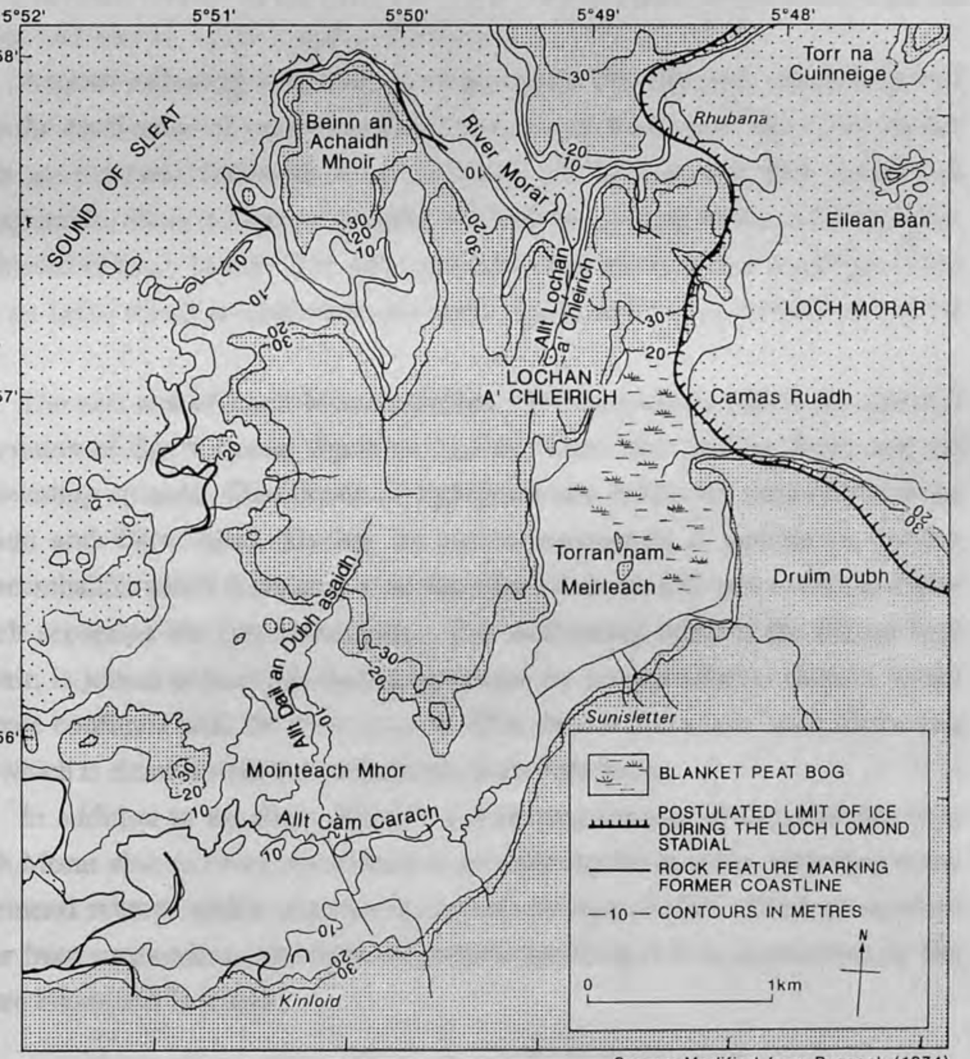
The western end of the loch is separated from the coastal sea-board, approximately 550 metres distant, by a narrow range of low hills orientated approximately due north-south in direction. The present outflow of the loch is via the River Morar. This river flows in a sinuous course from a northwestern point at the west end of the loch, passing through the narrow range of low hills, before finally descending in altitude and flowing over a rock sill at the Falls of Morar, where it debouches into the sea. The alignment of the hills which separate Loch Morar from the sea, generally corresponds with the strike of the Moine schist rock, which is mainly north-northeast to south-southwest in orientation. Within these hills there is located a small freshwater hill lochan, called Lochan a'Chleirich, which is situated at an altitude of approximately 30 metres OD.

The topographic relief and bathymetry of the west end of Loch Morar conveyed to Murray and Pullar (1910) the following impression: ".... It seems almost certain that the outlet of Loch Morar was at one time to the southwest because the col (i.e. hill) there does not rise more than 100 feet (30.5 metres) above the sea, and there is a narrow belt of comparatively flat ground running southwards towards the source of the burn (i.e. stream) called the Allt Cam Carach. It will be observed, by an examination of the depth map, that the deep water at the west end of the loch runs in the direction of this flat ground."

The col near the southwestern extremity of the loch attains a maximum elevation of approximately 25 metres OD, and extends in a southwest to westward direction, forming a broad plateau which slopes gently downward in elevation to the coast. This area presents a striking visual and topographic contrast with the surrounding terrain. The plateau is covered with an extensive development of ombrogenous *Sphagnum* bog which covers an area of several square kilometres. A series of boreholes made by the author has revealed that the development of peat exceeds 4m in depth, particularly in the vicinity of the rock knoll of the Torran nam Meirleach. Numerous streams which drain the high ground in this region become confluent as they pass in a seaward direction across this plateau. Several streams merge together to form a considerable stream, called the Allt Cam Carach, which traverses the plateau in a meandering course, directed approximately southwest-westward across the Mointeach Mhor, before finally debouching at the coast. The western part of the Morar Basin is illustrated in Figure 4.

The catchment area of the Morar basin is approximately rectangular in plan view. Indeed, the natural divide or watershed, i.e. where head-streams flow to separate river systems, follows the highest ground on both sides of Loch Morar, i.e. north and south Morar, respectively, and passes within 4.8 kilometres beyond the east end of Loch Morar, where it is limited by the high summits of Sgurr nan Coireachan (955 metres OD), Carn Mor (828 metres OD) and Sgurr na h-Aide (859 metres OD). The drainage area of the basin of the River Morar has been calculated to be 170 square kilometres (Murray and Pullar, 1910). The surface area of Loch Morar is 26.69 square kilometres, which comprises 15.7 *per cent*, or just over one-sixth, of the total area. The remaining area comprises several other freshwater lochs, including principally Loch Beoraid, Loch an Nostarie and Loch

Fig.4 THE WESTERN PART OF THE MORAR BASIN



Source: Modified from Peacock (1974)

Eireagoraidh, and a number of small lochans and streams on both sides of Loch Morar, up to an elevation of almost 610 metres OD, e.g. on the upper slopes of Math Bienn (summit, 710 metres OD) to the south of Loch Morar, which ultimately drain into Loch Morar.

A major inflow of water to Loch Morar occurs by way of the River Meoble. This river issues from Loch Beoraid, which is situated at an elevation of 51.2 metres OD, and almost 4.8 kilometres due south of Loch Morar. During its course, the River Meoble is joined by several large streams, which become confluent during its descent. Before doubouching, the river flows into the Loch Morar at a bay called Camus Luinge, which is situated on the south shore at a point almost mid-way along the length of the loch.

Another inflowing stream of significant size is the Allt Loin, which is formed from the confluence of streams exiting from several freshwater lochs, principally Loch an Nostarie (situated at an elevation of 27.2 metres OD) and Loch Eireagoraidh, along with some smaller hill lochans situated within 3.2 kilometres northward of Loch Morar. The Allt Loin flows into the loch at a small bay called Bun an Loin, which is situated on the north shore, near to the western end of the loch.

The east end of Loch Morar receives inflowing streams from the adjacent mountains of Sgurr Breac, Sgurr na h-Aide, Carn Mor and An Stac, and the surrounding uplands. One stream of significant size drains the slopes of Sgurr na h-Aide and Carn Mor. During its course westwards it gathers in Lochan Gaineamhaick, which is situated at an elevation of above 150 metres OD, in a glen which separates the two mountains. The outflowing stream, the Ceann loch Morair, is joined at intervals during its course by several smaller streams which become confluent with the main stream. This stream flows into Loch Morar at a bay which is situated near the northeastern part of the loch.

In addition to the River Meoble and several streams of considerable size, Loch Morar also receives water from numerous smaller sources, including many ephemeral streams which arise during periods of high rainfall. The loch receives water from surrounding catchment area which is estimated to be approximately 143 square kilometres in extent.

CLIMATIC CONDITIONS OF THE MORAR BASIN

The climate of the Morar Basin, in common with the adjoining landmass and coastal sea-board of the western highlands of Scotland, is markedly oceanic and mild. A succession of cyclonic depressions track from the Atlantic Ocean, which bring cloud, wind and moderate to heavy rain inland throughout the year. The prevailing wind is south-westerly in direction and often strong to gale force. The mean annual precipitation ranges between 1,500-2,500 millimetres at sea-level, increasing to between 2,500-3,750 millimetres at higher altitude, and in a gradient from west-east across the Morar Basin. Cloud cover is correspondingly highest in the east. The mean annual number of wet days, on which at least 1.00mm rain falls in 24 hours, ranges between 200-220 on the coast, to over 220 across the basin. Although rainfall is generally well distributed throughout the year, there is often a marked winter maximum and a spring or early summer minimum. There is usually a potential water surplus, except during unusually dry periods, which occur notably in spring and early summer. When precipitation falls as snow it melts rapidly at low altitudes, and the duration of snow cover is estimated to be less than 30 days *per annum*, but this increases markedly at higher altitude. Semi-permanent snow beds are poorly developed on ground above 760 metres beyond the eastern end of Loch Morar. Snow patches may often persist into spring months, particularly on high ground with a northerly aspect. Local snow patches occurring in early May on Druim a'Chuirn, south of Loch Morar, are discernible in Plate 2.

The North Atlantic Drift exerts a significant influence on the prevailing climate, and results in relatively mild winters and cool summers. Mean monthly temperatures exhibit seasonal gradients across the Morar Basin. Thus, the mean temperature of the coldest month, which is February, ranges between 1.7°C on the west coast to 1.1°C in the east, while the mean temperature of the warmest month, which is July, ranges from 13.5°C in the Sound of Sleat to 14.0°C south-east of the basin. The difference between the mean temperature of the coldest month and the mean temperature of the warmest month ranges between 12.2°C on the west coast to 12.9°C in the east. The mean maximum July temperature ranges between 16.1°C to 18.3°C from west to east across the Morar Basin.

The mean monthly temperature data and mean annual precipitation data for the Morar Basin are derived from Meteorological Office records for the period 1941-1970, while the mean annual number of wet days are derived from Meteorological Office records for the period 1951-1960 (HMSO, 1978).

SOILS OF THE MORAR BASIN

The Moine schist rocks which occur in the catchment area of the Morar Basin, are predominantly micaceous but non-calcareous, and these give rise to mountain soils with an illusory appearance of fertility (McVean and Ratcliffe, 1962). In general, the soils occurring in well drained areas, upon accumulations of glacially derived sediments originating from the Moine rocks and including quartzite, are often sandy and strongly leached, and exhibit well developed podsolized profiles. The sub-alpine soils, which generally occur above 760 metres OD, tend to be skeletal and frequently consist of a layer of acidic mor humus overlying gravel. On poorly drained ground gleyed soils and peat are often widespread, particularly in areas with shallow gradients. In contrast, the soils occurring at sites with relatively improved base status, particularly in flushed areas, are typically acid brown earths, while peat is relatively rare.

The vegetation associated with these soil types is also distinctive. Thus, coniferous Scots pine woodland on the islands in Loch Morar, and *Calluna* heath on the surrounding hills are generally associated with well developed podsols, while the broad-leaved deciduous woodland communities throughout the Morar Basin are typically associated with acid brown earth soils. Blanket bog communities dominated by *Sphagnum* mosses are associated with blanket peat, which is often several metres in depth, particularly on gently sloping terrain at relatively low altitude. Arctic-alpine vegetation is mainly associated with the skeletal sub-alpine soils which develop under extreme climatic conditions at relatively high altitude, particularly in mountainous areas and high ground surrounding the eastern part of Loch Morar.

CHAPTER 3

INDIGENOUS HIGHLAND WOODLAND COVER

The destruction of the original primary forest cover of Scotland is now virtually complete, while the advent of re-afforestation programmes is tending increasingly to obscure the last evidence of the native forest pattern (McVean, 1964a, *in* Burnett, 1964). Approximately 9 *per cent* of the British Isles currently supports woodland trees. Significantly, only approximately 2 *per cent* of the land area of the British Isles currently supports native trees (Bunce, 1982; Pears, 1985). Despite this extremely reduced cover *circa* 3,000 square kilometres, the current range of native tree species is, nevertheless, diverse and includes broad-leaved deciduous species, e.g. oak, *Quercus robur* and *Q. petraea*; ash, *Fraxinus excelsior*; rowan, *Sorbus aucuparia*, along with coniferous species, e.g. Scots pine, *Pinus sylvestris*, and yew, *Taxus baccata*.

The former climax forests of the British Isles have been considerably reduced in extent by anthropogenic activity, dating from at least 5,000 years ago and generally corresponding with the Neolithic cultural period. The few surviving remanents of natural climax forest are now represented by quasi-natural communities of woodland which are generally modified derivative remanents of climax forest eco-systems. These merit conservation not only as eco-systems of scientific interest but as living representatives of the former forests of Scotland (Birks, H.J.B., 1977).

The present geographical distribution of native trees in Scotland was examined in detail by McVean and Ratcliffe (1962). This study revealed that although the current native woodland cover in Scotland is highly fragmentary, there are, nevertheless, numerous surviving communities of variable size, often occurring upon islands in lochs (McVean, 1958), in ravines, river gorges and on steeply sloping ground.

The current geographical distribution of native oak, *Quercus petraea* and Scots pine, *Pinus sylvestris* within Scotland at least, evidently correlates with apparent differences in latitude, topography, climate and geology; other native tree species, in particular birch, *Betula* species and alder, *Alnus glutinosa*, exhibit a rather more general pattern of distribution within their specific altitudinal ranges (Burnett, 1964).

While stands of native Scots pine, *Pinus sylvestris* var. *scotica* may be reliably distinguished from self-seeded introductions in Scotland, it is often difficult to ascertain whether stands of oak trees comprise either naturally occurring or introduced *Quercus* species. This difficulty has been compounded to a certain extent as a result of former planting of *Quercus robur* in districts, and upon soils, which would naturally support *Q. petraea*. Historical accounts indicate that *Quercus robur* seed from England was frequently introduced into Scotland and cultivated for its superior tannin-rich bark. Furthermore, *Q. robur* also appears to have been planted at sites which formerly supported *Q. petraea* under coppice management (Jones, 1959). Thus, pure stands of *Q. robur* may have arisen in some places as a direct result of deliberate selection by foresters (Anderson, 1950). Natural hydridization has also arisen between the two British oak species throughout northern Britain. Indeed, a large number of *Quercus* trees occurring in Scotland appear to be intermediate between *Q. petraea* and *Q. robur*. Hence, the taxonomic status and geographical distribution of native stands of oak is currently unclear.

The birch trees, *Betula pubescens* ssp. *pubescens* and spp. *odorata* and *B. pendula* are the commonest trees of Scotland (McVean, 1964a). Their taxonomic separation is difficult, therefore the distribution of the species and sub-species is imperfectly known. *Betula pubescens* often occurs as pure stands above the limit of oakwood in the north and west. *B. pubescens* ssp. *odorata* is generally widespread in northern and mountainous areas, while *B. pendula* is rare in northern Scotland.

In view of these considerations, McVean and Ratcliffe (1962) reconstructed the potential geographical distribution of the predominant forest cover, comprising oak, pine and birch, which existed in Scotland, prior to the widespread forest clearances associated with the Neolithic Period. A map indicating the principal potential vegetational regions of Scotland and the main tendencies of woodland distribution is illustrated in Figure 5.

The reconstruction of the pattern of potential tree cover which existed in Scotland prior to widespread forest clearances revealed the following general points:

(1) Pine forest dominated by *Pinus sylvestris* ssp. *scotica* occurred predominantly in the central and north-east Highlands, extending up to approximately 610 metres altitude.

(2) Oak forest dominated by *Quercus* spp. occurred predominantly in southern Scotland, the Midland Valley, south-west Argyllshire, the Great Glen and its tributaries, and all the larger hills and valleys which penetrate the Highlands from south and west, extending up to approximately 300 metres altitude.

(3) Birch forest and scrub dominated by *Betula* spp. occurred predominantly in the far north and west of Scotland, while elsewhere forming a distinct zone

> situated altitudinally above the pine and oak forests; some hill slopes also supported a zone of pine between the oak and birch forest.

Evidently, nearly the entire land area of mainland Scotland, with the exception of the highest mountain summits, potentially supported some form of tree cover (Map A *in* McVean and Ratcliffe, 1962), in striking contrast with the currently diminishing and highly fragmentary woodland cover in Scotland (Map B *in* McVean and Ratcliffe, 1962).

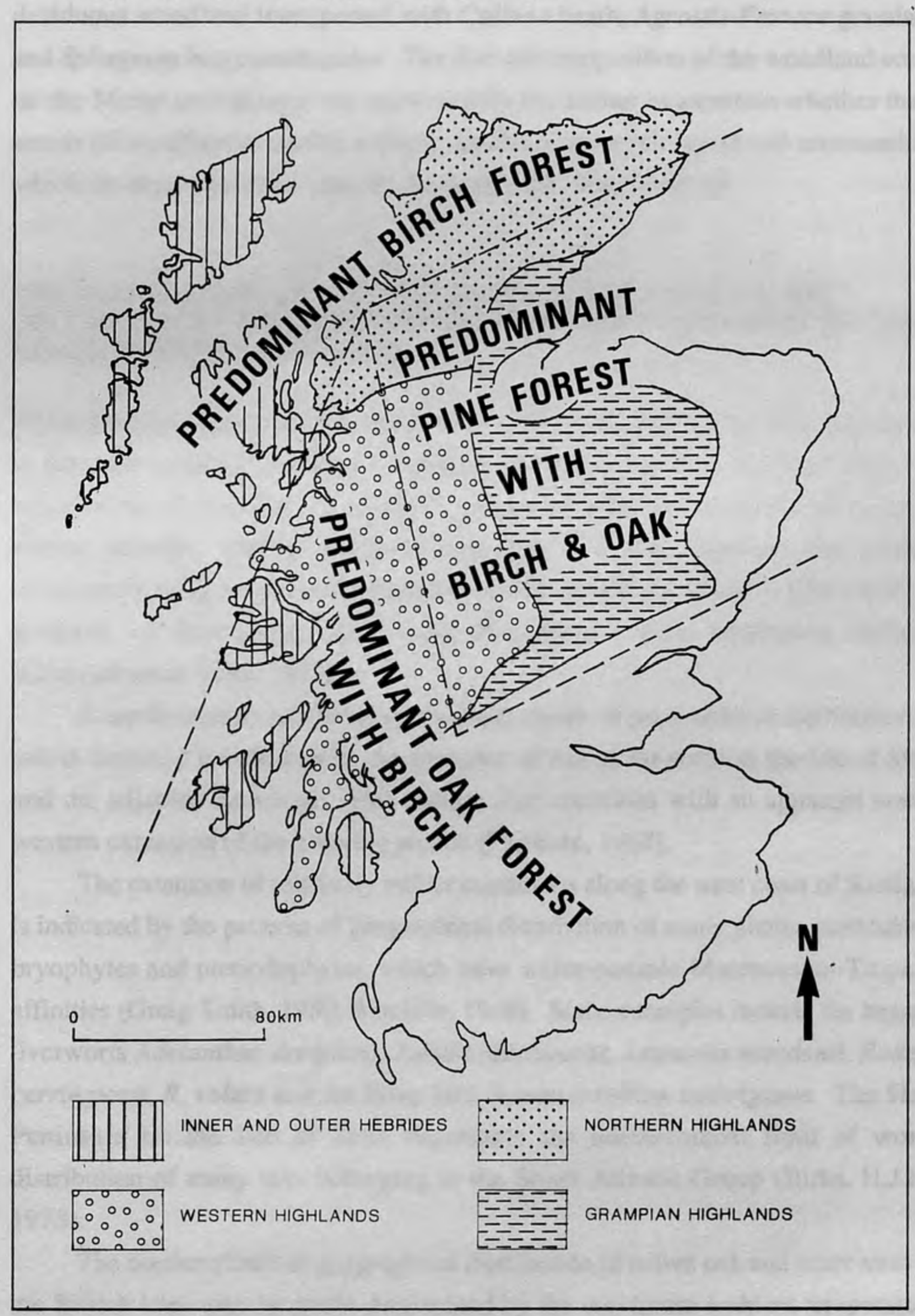
REMANENT WOODLAND COMMUNITIES ON ISLANDS IN THE SCOTTISH LOCHS

A number of principal Scottish lochs and hill lochans feature emergent islands, which may be either isolated or aggregated into archipelagos. These islands often support scrub and woodland communities, which present a striking visual and floristic contrast with the surrounding terrain, particularly where there is a predominance of *Calluna* heath and *Sphagnum* bog communities in the catchment area.

Many of the islands in these lochs have attracted human interest and exploitation, in some cases dating from the Mesolithic period, e.g. stone artefacts attributed to the Late Mesolithic Period have been recorded from the island of Inchlonaig and from sites near the mouth of Glen Finlas, Loch Lomond (Stewart, 1979). In particular, the larger islands have been used as sources of timber and subsequently, for summer grazing within forest clearings. Some islands were also periodically occupied and settled; when these island settlements were subsequently abandoned, the open ground was recolonized by forest trees. Depending upon geographical location and aspect, mor peat formation and native Scots pine often correlate with sites of gravel and coarse sand substrata, while acid brown earth soil and stands of deciduous trees often develop at sites with relatively finer mineral substrata (McVean 1958).

The surviving fragments of native or quasi-native woodland communities which occur on these islands, while generally self-sown, are particularly significant. Although these plant communities are not wholly unmodified remanents of primary climax forest, they are nevertheless very similar in floristic composition and structure to the best examples of surviving self-sown woods of birch, oak and pine which occur on the mainland of Scotland. Moreover, they resemble primary climax forest, particularly in relation to the density of the stands

Fig:5 POTENTIAL WOODLAND COVER UNDER NATURAL CONDITIONS FOR THE HOLOCENE IN SCOTLAND



Source: McVean & Ratcliffe (1962); Burnett (1964) of trees, frequency of occurrence of shrubs and understorey vegetation, and luxuriance of the field layer (McVean, 1958).

The dense stands of Scots pine on the island archipelago in Loch Morar provide a spectacular visual and floristic contrast with the surrounding landscape of the Morar Basin, which supports fragmentary communities of broad-leaved deciduous woodland interspersed with *Calluna* heath, *Agrostis-Festuca* grassland and *Sphagnum* bog communities. The floristic composition of the woodland cover on the Morar archipelago was examined by the author to ascertain whether these stands of woodland resemble indigenous *Pinus sylvestris* woodland communities which are described from other locations in north-west Scotland.

THE POSSIBLE INFLUENCE OF CLIMATIC CONDITIONS ON THE GEOGRAPHICAL DISTRIBUTION OF NATIVE OAK AND SCOTS PINE IN NORTH-WESTERN SCOTLAND

Meteorological records for the period 1941 to 1970 indicate that between September to May the monthly temperature range is relatively higher in north-western and western coastal locations in Scotland, compared with central inland locations at similar latitudes. During the period from June to August, however, the monthly temperature range is relatively higher in central locations. There is also a distinct gradient of decreasing July mean temperature with increasing latitude (Climatological Atlas, 1952).

A north-western extension of the main centre of geographical distribution of oak in Scotland is indicated by the presence of oak as far north as the Isle of Skye and the adjacent mainland. This pattern also coincides with an apparent north-western extension of the growing season (Fairburn, 1968).

The extension of relatively milder conditions along the west coast of Scotland is indicated by the patterns of geographical distribution of many plants, particularly bryophytes and pteriodophytes, which have warm-oceanic Macronesian-Tropical affinities (Greig-Smith, 1950; Ratcliffe, 1968). Some examples include the hepatic liverworts *Adelanthus decipiens, Jubula hutchinsiae, Lejeunea mandonii, Radula carringtonii, R. voluta* and the filmy fern *Hymenophyllum tunbrigense*. The Sleat Peninsula on the Isle of Skye represents the northernmost limit of world distribution of many taxa belonging to the South Atlantic Group (Birks, H.J.B., 1973).

The northern limit of geographical distribution of native oak and other trees in the British Isles may be partly determined by the maximum ambient temperature (Williams, 1977). An interesting example is provided by the small-leafed lime, *Tilia cordata*. This species currently attains its northern geographical limit in the

Cumbrian Lake District, where significantly it produces seed only rarely. The apparent infertility of *Tilia cordata* at this northern latitude in the British Isles is largely attributable to cool ambient summer temperatures. The July temperature maxima appear to be too low and insufficient in duration to allow the growth of pollen tubes for fertilization and, subsequent development of ovules, during the reproductive phase of this species. Only during years with extremely warm summers, e.g. during 1976, have these populations been reported to produce mature fruits. The reproductive success of these trees may be a useful indicator of climatic change in Britain (Pain, 1989).

The geographical distribution of native Scots pine may also be determined by ambient temperature regime and its effect during the reproductive phase of the species (Salisbury, 1939; Carlisle and Brown, 1968). The geographical limit of Scots pine in north-western Scotland may be additionally influenced by mean annual precipitation and a high precipitation to low evapo-transpiration ratio. Thus, relatively lower summer mean temperatures in western and coastal districts compared with central inland districts may reduce reproductive success, while the extensive development of waterlogged soils and blanket bog vegetation renders ground unsuitable for successful germination of seeds, which consequently reduces population regeneration.

THE PHYSIOGNOMY OF WOODLAND VEGETATION IN THE SCOTTISH HIGHLANDS

Forests and woodlands exhibit a distinctive physiognomy or primary morphology which reflects the characteristic features and appearance of the plant community. Indeed, a forest exhibits a greater degree of structural diversity than any other major eco-system, with separate distinctive layers of vegetation. The native woodland communities occurring in the Scottish Highlands are typically multi-layers in vertical profile, with generally distinctive tree, shrub, field and ground layers, respectively.

(1) THE TREE LAYER

The tree layer is the predominant structural component of a forest or woodland, and it is defined as the aggregation of woody species over 5 metres in height which form the canopy.

Although forests and woodland are not comprised solely of stands of trees, the tree layer, nevertheless, exerts a significant influence on the whole eco-system.

In the Scottish Highlands, the native Scots pine, oak and birch frequently represent the tallest plant taxa and, therefore, the dominant physiognomic elements in woodland communities. Furthermore, these taxa also exert a significant ecological influence and therefore represent the ecological dominants in the woodland communities.

Because trees grow to maturity over a period of decades or centuries, the cycle of death and regeneration in a natural stand is irregular in time and space, and this gives rise to a varied structure and age distribution of the tree layer, and often an accumulation of decaying timber on the ground. The height and growth form of trees are greatly influenced by environmental factors, including soil depth, exposure to wind and density of individual trees.

The age, density of individuals and species characteristics of the trees partly determines the floristic composition of the subsidiary layers within the woodland community. Thus, it is possible to identify woodland by the array of trees which form the tree canopy, and to sub-divide the different woodland communities on the basis of their associated assemblages of shrubs, herbs and ground flora (Bunce, 1982). Prior to extensive anthropogenic interference, the floristic composition of the forest cover in the British Isles was determined primarily by latitude, climatic conditions, topography and geology, while local variations were often determined by edaphic conditions.

(2) THE SHRUB LAYER

The shrub layer includes all plants between 1 metre and 5 metres in height. The development of this layer depends on the influence of the dominant trees, climate, soil conditions and forestry practice. The woodland communities in the Scottish Highlands are commonly devoid of a shrub layer, often due to intensive grazing. However, in ungrazed woodland where the tree canopy is open, there is often a local abundance of juniper, *Juniperus communis*, particularly within Scots pine and birch woodland respectively, while hazel, *Corylus avellana*, is often well developed within mixed oak and birch woodland.

(3) THE FIELD LAYER

The field layer is characterized by a dense growth of small shrubs, herbaceous plants and pteridophytes, usually less than 1 metre in height. The taxa which occur in this layer, while largely independent of the tree and shrub layers, nevertheless, depend on the shade and high humidity which are conferred by the overhead canopy. There is also an important ecological separation between grazed and ungrazed field layers.

(4) THE GROUND LAYER

The ground layer is often associated with conditions of moderate shade within woodland, particularly where old and senescent trees have fallen through the tree canopy. The ground beneath is often covered with bryophytes and a variety of lichens which comprise the ground layer. The luxuriance of this layer is a notable feature of many native woodlands in the Scottish Highlands.

The taxa which comprise the field layer and ground layer in a woodland are particularly sensitive to anthropogenic interference. A range of Atlantic taxa, including filmy ferns, bryophytes and lichens require shade and high relative humidity which are conferred by the overhead canopy. Many of these taxa evidently perish and disappear from the woodland where the tree or shrub layers are reduced or destroyed.

(5) EPIPHYTIC VEGETATION

Although a vascular epiphytic flora is very poorly represented in woodland communities throughout the British Isles, cryptogamic plants, principally lichens and bryophytes, form extremely diverse epiphytic (corticolous) communities upon the bark of woodland trees, particularly in areas which are remote from sources of atmospheric pollution. The woodlands of western Scotland are notable for their unique representation of oceanic lichen species and epiphytic lichen communities. Significantly, the presence of selective epiphytic lichen taxa may be indicative of ecological continuity of high tree cover, and hence indicative of temporal continuity of woodland, in certain situations (Rose, 1976). The floristic composition and phytosociology of the epiphytic lichen flora of these woodlands is discussed in Chapter 4.

PHYTOSOCIOLOGICAL ASPECTS OF VEGETATION COVER IN THE SCOTTISH HIGHLANDS

A novel method of describing stands of vegetation was developed by McVean and Ratcliffe (1962). Floristic data from the analysis of plant communities in the Scottish Highlands (McVean and Ratcliffe, 1962) revealed that floristic variation in Highland vegetation is virtually continuous. Furthermore, gradual spatial change is common. Indeed, even where local discontinuities exist, it is usually possible to find a complete series of intermediates to link any two related types, if a wider geographical area is sampled.

Thus, McVean and Ratcliffe selected vegetational "reference points" of sufficient number and diversity to represent the total range of floristic variation presently occurring in Scottish Highlands. These "reference points" were called *noda* (singular *nodum)*, a term which was initially used by Poore (1955) to describe abstract vegetational units. The sampling method was based upon two criteria: firstly, that a large number of reference points are selected within close proximity to each other, and within heterogeneous and floristically-rich vegetation where spatial change was abrupt, and secondly, that a small number of reference points are selected at some distance apart, within relatively homogeneous and floristically-poor vegetation, where spatial change was gradual.

Where two or more noda exhibit sufficient homogeneity and organization they can be raised to the status of an *association.* The ratio between the number of species in the two highest frequency or constancy classes, is used as an Index of Homogeneity. The term *nodum* refers to any described vegetation type which does not merit the rank of an association, i.e. it is an abstract term which is based upon the common features of a number of particular stands of vegetation. The term *community* on the other hand, refers to the real vegetation, i.e. a particular stand of vegetation. Where there is an obvious discontinuity in the floristic variation within a vegetation unit, e.g. several species appear or disappear collectively from censuses taken in the field, and the extent of the discontinuity does not warrant the status of separate units or noda, the distinctive groups are described as separate *facies.* In some cases, facies may be distinguished by the presence or absence of just a few noteworthy species, or merely by a change in the dominance of one or two species.

McVean and Ratcliffe (1962) named the different associations and noda according to their prominent species or genera (dominants or constants). The conventional suffix *-etum* is used to denote associations, with the addition of a non-floristic qualification where this is desirable. Facies are distinguished within an association by the use of the suffix *-osum*, which is applied to the most prominent species or group of species, e.g. *Pinetum Hylocomieto-Vaccinetum triquetrosum*; the naming of other facies is given in an anglicized form. The constants of an association are termed the *association element.* The use of constants and dominants together has been found to be the most useful means of characterizing a nodum.

Braun-Blanquet (1932) divided the characteristic species of a vegetation type into the following categories: *exclusive* species, which are either completely or almost completely confined to one community; *selective* species, which are found most frequently in one community while occurring sparsely in others, and *preferential* species, which occur more or less abundantly in several communities, while attaining their optimum development in one particular community. The term characteristic species *sensu* Braun-Blanquet (1932) was not employed by McVean and Ratcliffe (1962).

While the system of noda devised by McVean and Ratcliffe (1962) does not attempt to describe completely the entire range of vegetation presently occurring in the Scottish Highlands, it nevertheless permits any randomly selected plant community to be assigned to a specifically described vegetational unit or nodum, or at least, to an intermediate position between two units or noda.

WOODLAND COVER IN THE MORAR BASIN

The geographical distribution of the woodland cover in the Morar Basin, and the floristic composition *sensu* Birks, H.J.B. (1977) and phytosociology of the principal woodland communities *sensu* McVean and Ratcliffe (1962) are described below.

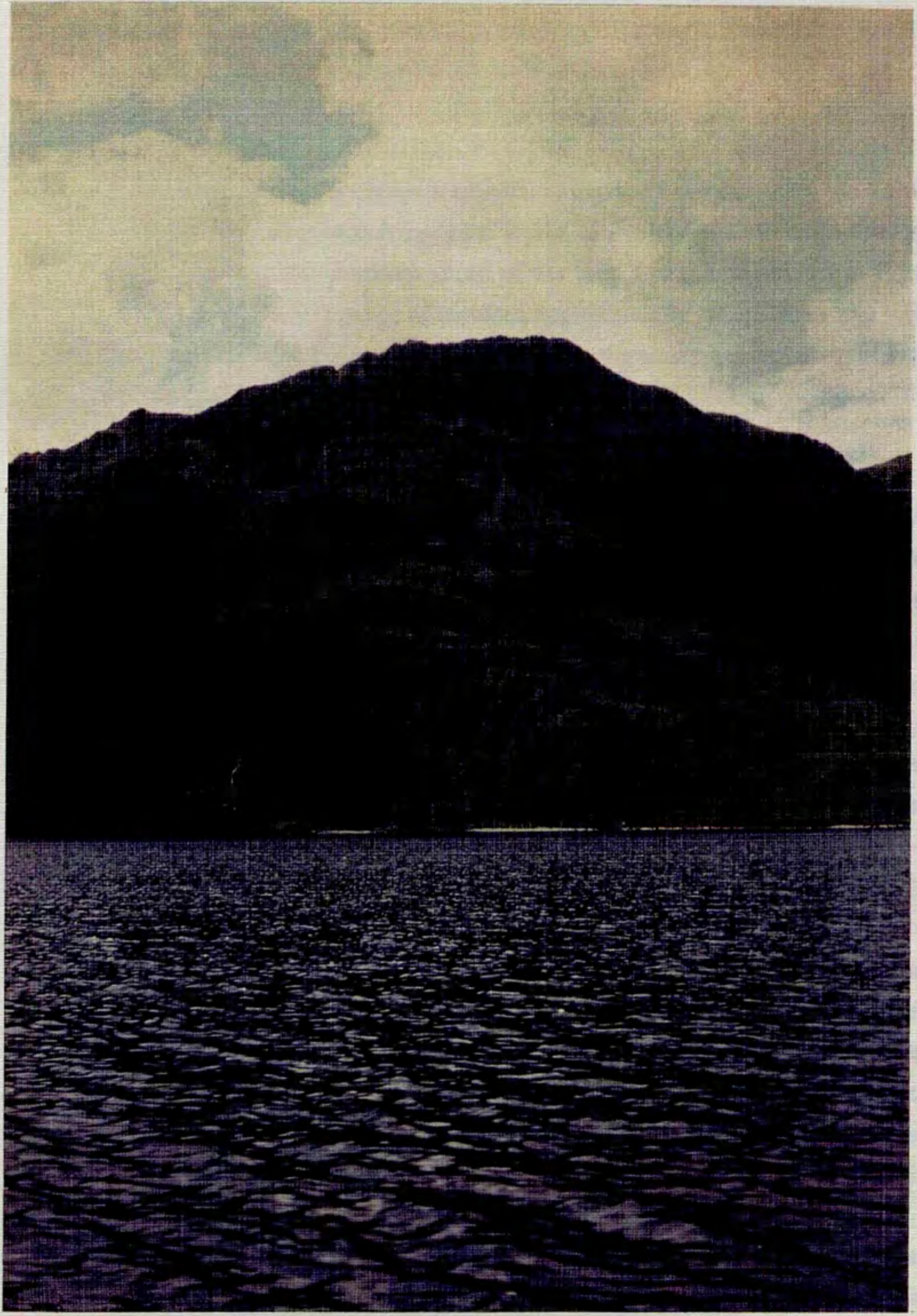
THE GEOGRAPHICAL DISTRIBUTION OF WOODLAND COVER IN THE MORAR BASIN

The woodland cover of the Morar Basin consists predominantly of mixed oak and birch communities, which survive at a number of sites within the catchment area of Loch Morar. A view of native birch and oak woodland on a hillside near Coille Allmha, near Loch Morar, is illustrated in Plate 3. The woodland cover of the Morar Basin therefore corresponds with the zone of predominant oak forest with birch *sensu* McVean and Ratcliffe (1962), at least in the context of its geographical distribution. A significant exception is woodland cover of the island archipelago in Loch Morar, which is dominated by Scots pine communities. The geographical distribution of the principal areas of native woodland in the Morar Basin is illustrated in Figure 3.

SITES OF BROAD-LEAVED DECIDUOUS WOODLAND WITHIN THE MORAR BASIN

The principal areas of broad-leaved deciduous woodland occur at three main locations described below (sites i-iii) which separately cover an area of between 30 to 50 hectares, while the remaining areas of woodland cover (sites iv-ix) are generally far smaller in extent, and typically cover an area of just a few hectares.

Plate 3 Native birch and oak woodland near Coille Allmha, South Morar



(i) KINSADEL

This woodland community is situated approximately 500 metres from the western end of Loch Morar, and due south of the Kinsadel homestead. The woodland surrounds a small hill lochan called Lochan a'Chleirich (*circa* 30 metres OD) and extends around the nearby estuary of the River Morar. The woodland covers an area of approximately 50 hectares, within an altitudinal range of between 10 to 90 metres OD.

(ii) DRIUM DUBH

This woodland community is situated at the south-western point of Loch Morar. The woodland fringes the banks of the bay at Camus Ruadh and extends along the southern shore of the loch and the adjacent hill-sides within an altitudinal range of between approximately 10 to 200 metres OD. A view of native birch and oak woodland at the south-western end of Loch Morar is illustrated in Plate 4.

(iii) COILLE POLL NAN UISGEANAN

This woodland community is situated along the southern shore of Loch Morar, at a point lying approximately mid-way between the eastern and western ends of the loch. The woodland extends over the hill-sides, within an altitudinal range of between approximately 20 - 300 metres OD.

Several smaller areas of oceanic broad-leaved deciduous woodland occur elsewhere on the hills surrounding Loch Morar. The majority occur along the southern shore of the loch at the following locations:

(iv) COILLE ALLMHA

This woodland community is situated westward of Coille Poll Losgannan (cited above). The woodland extends along the southern shore of Loch Morar and the adjacent hill-sides, with an altitudinal range between a lower limit of approximately 10 - 30 metres OD and an upper limit of between 110 to 150 metres OD.

(v-vi) DRIUM A'CHUIRN AND COILLE A'CHUIRN MHOIR

Several small woodland communities are situated along the southern shore of Loch Morar, within 5 kilometres of the eastern end of the loch. These communities occur on a hill range called Druim a'Chuirn, extending from the southern shore up to approximately 250 metres OD altitude. An adjacent woodland community at Coille a Chuirn Mhoir is situated approximately 3 kilometres from the eastern end of the loch. This woodland area extends along the southern shore, within an altitudinal range between approximately 10 to over 350 metres OD, which represents the highest altitudinal limit for oceanic broad-leaved deciduous woodland within the catchment area of Loch Morar.

Two small areas of oceanic broad-leaved deciduous woodland occur on the hills above the northern shore of Loch Morar at the following locations:

(vii) SOUTH TARBET BAY

This woodland community is situated slightly eastward of a point lying mid-way between the eastern and western ends of the loch. This woodland extends from the northern shore up to approximately 150 metres OD altitude.

(viii-ix) BRACORA AND BRACORINA

This woodland community is situated approximately 4 kilometres from the western end of the loch, on steeply sloping ground, within an altitudinal range between approximately 20 to 80 metres OD. A small stream descends over waterfalls within the woodland before debouching into Loch Morar. The tree canopy is particularly well developed in the vicinity of this stream and high relative humidity prevails within the woodland, even during the relatively drier spring months. Several splendid old *Quercus petraea* trees with distinctive spreading crowns occur above the bay at Bracorina. A view of these trees is illustrated in Plate 9. The epiphytic flora is often very well developed upon the boughs and trunks of broad-leaved deciduous trees within these woodlands, typically at lower altitude and within relatively undisturbed areas. These woodlands also exhibit a wide variety of pteridophytes, bryophytes, liverworts and lichens, including several warmth and moisture-dependent species which are growing close to their northernmost locations in the world, e.g. the filmy fern *Hymenophyllum tunbrigense* and the liverwort *Adelanthus decipiens*.

Plate 4 Native birch and oak woodland by Camus Ruadh, at the south-western end of Loch Morar

THE FLORISTIC COMPOSITION OF MIXED OAK AND BIRCH WOODLAND COMMUNITIES

Deciduous woodlands are multi-layered, usually with distinctive tree, shrub, field and ground layers. They generally require a climate which has a growth period of four to six months, and a cool but mild winter period of three to four months, when their leaves are shed (Polunin and Walters, 1985). Surviving examples of native deciduous woodland are highly fragmentary within western and southern Scotland. These woodlands exhibit a very distinctive floristic composition under the humid and mild oceanic climatic conditions which prevail along the western coastal sea-board of Scotland. The predominant woodland cover occurring within the Morar Basin comprises oceanic deciduous woodland communities, which typically exhibit a tree layer dominated by *Quercus petraea* and *Betula pubescens* ssp. *odorata.* Hybrids of *Q. petraea* and *Q. robur* are also occasionally present. Other taxa which occur frequently within these woodland communities include *Sorbus aucuparia, Alnus glutinosa, Ilex aquifolium* and occasionally *Populus tremula,* along with *Salix cinerea* ssp. *oleifolia, S. caprea, Prunus padus, P. spinosa, Viburnum opulus, Hedera helix* and *Rubus fruticosus.* The shrub layer is frequently dominated by *Corylus avellana* which forms an extensive cover, particularly where there are open areas in the tree canopy, and upon base-rich soils where it may be occasionally accompanied by *Fraxinus excelsior.* The shrub *Juniperus communis* is, however, extremely rare; a solitary mature specimen of *J. communis* ssp. *communis* was recorded growing leeward of a rocky promontory at Inbhir Beag, east of Bracorina, on the northern shore of Loch Morar.

The field layer of these woodland communities appears to be significantly influenced by the intensity of grazing activity arising from wild herbivores and domesticated livestock. Thus, areas which are generally inaccessible to grazing animals exhibit a field layer which comprises *Vaccinium myrtillus, Luzula sylvatica* and several pteridophyte taxa commonly including *Blechnum spicant, Dryopteris affinis, D. dilatata, Oreopteris limbosperma, Phegopteris connectilis* and a generally rare species *Dryopteris aemula,* which was recorded in woodland near Lochan a'Chleirich (Rose, 1978). Herbaceous taxa including *Potentilla erectus, Oxalis acetosella, Digitalis purpurea,* and *Viola riviniana* are also locally abundant.

Where the woodland develops in flushed areas or elsewhere upon basic substrata the field layer of ungrazed woodland typically supports a variety of characteristic herbaceous taxa, including *Anthoxanthum odoratum, Anemone nemorosa, Hyacinthoides non-scripta, Oxalis acetosella, Primula vulgaris* and *Sanicula europaea. Vaccinium myrtillus* is however, occasional in these communities. The taxa *Oxalis acetosella, Viola riviniana* and *Primula vulgaris* are locally abundant in the woodland surrounding the River Morar.

In areas of woodland which are subjected to intensive grazing activity the field layer comprises predominantly *Pteridium aquilinum* and *Calluna vulgaris,* with a reduction in *Vaccinium myrtillus* and *Luzula sylvaticirca* There is often a corresponding increase in some grass taxa, in particular, *Deschampsia flexuosa* and *Molinia caerulea* along with the herb *Galium saxatile.* Other taxa which occur frequently within the field layer of these woodlands include *Melampyrum pratense* and *Teucrium scorodonia.*

The ground layer within these woodlands is floristically very rich, particularly covering boulders, and includes the bryophytes *Dicranum scoparium, D. majus, Hylocomium splendens, H. brevirostre, Mnium hornum, M. undulatum, Rhytidiadelphus loreus, R. triquetrus, Thuidium tamariscinum, Hypnum cupressiforme* vars., and *Pleurozium schreberi* along with many ocean taxa of liverworts, including *Adelanthus decipiens,* saxicolous lichens, and the filmy ferns *Hymenophyllum tunbrigense* and *H. wilsonii.* The prevailing oceanic climate of the west coast of Scotland also favours the development of a distinctive and frequently luxuriant woodland epiphytic flora. These epiphytic communities comprise filmy ferns, hypnaceous bryophytes, liverworts and a remarkable range of corticolous lichens. Epiphytic bryophytes recorded on woodland trees near Lochan a'Chleirich (Rose, 1978) included the taxa *Ulota bruchii* and *U. phyllantha,* along with *Dicranum scoparium* growing on *Betula, Hypnum cupressiforme* var. *cupressiforme* growing on *Quercus, H. cupressiforme* var. *filiforme* growing on *Quercus, Betula* and *Salix,* and *Isothecium myosuroides* growing on *Quercus, Corylus* and *Salix.* The epiphytic corticolous lichen communities occurring in these deciduous woodlands are described in Chapter 4.

The ground within these woodlands in frequently strewn with large boulders and block scree, which effectively reduces the area available for the development of a continuous soil layer. In favourable situations, however, the soils which develop are either freely-draining podsols or acid brown earth soils.

Within the Morar Basin, the birch *Betula pubescens* ssp. *odorata* is the commonest tree, often forming pure stands or occurring in mixed stands with *Quercus petraea.* Communities dominated by birch are particularly well developed on north-facing slopes ranging from sea-level to approximately 250 metres OD altitude. Communities dominated by the oak *Quercus petraea* and mixed stands containing birch are common in the southern and western parts of the Morar Basin.

The oak trees within the catchment area of the Morar Basin are often well developed at low altitude, particularly surrounding Loch Morar. Furthermore, in sheltered situations, a dense tree canopy encourages high relative humidity to develop within the woodland, particularly in the vicinity of flowing or standing water. Under these conditions the boughs of the trees often support a remarkably diverse epiphytic flora. With increasing altitude, the oak trees evidently decline in vigour, height and girth. Furthermore, the epiphytic flora also becomes generally impoverished. These phenomena have been cited as typifying the mixed oak woodland communities of western Scotland. The effect of increasing exposure and rainfall at higher altitudes may significantly influence the habit of the oak trees and the respective epiphytic flora (Rose, 1977a).

BIRCH WOODLAND COMMUNITIES

Some woodland communities within the Morar Basin exhibit pure stands of *Betula pubescens* ssp. *odorata*, which often contain a well developed shrub layer of *Corylus avellana*, while significantly, *Quercus* species only form an occasional element in the woodland cover. This may reflect a general reduction in the frequency of occurrence of native *Quercus* towards the north-western limit of its geographical distribution in Scotland. Significantly, the north-western extension of the main area of geographical distribution of oak in Scotland broadly coincides with the Morar Basin and the adjacent Isle of Skye. Furthermore, the floristic composition of these communities shares several features in common with the birch forest zone *sensu* McVean and Ratcliffe (1962).

The principal floristic characteristics that separate the native *Betula* tree species are summarized in Table 2. These data were kindly provided by Dr Edward Lodge, University of London.

In northern Scotland and the Western Isles, the climatic regime is dominated by prevailing westerly and south-westerly winds. The prominent effect of exposure to the wind is further exaggerated with increasing altitude in upland areas. Although a number of tree species appear to be unable to tolerate these conditions, birchwood communities comprising mainly *B. pubescens* ssp. *odorata* and *Corylus avellana* scrub appear to thrive successfully; wet habitats are frequently colonized by *Salix*-carr woodland and *Alnus glutinosa*. *Betula pubescens* ssp. *odorata* has a predominantly western distribution, in Scotland at least, with an altitudinal range from sea-level up to approximately 610 metres OD. This tree species is tolerant of moderately wet regions, occurring typically, although not exclusively, on base-deficient soils, including freely-draining podsols and acid brown earths.

The birchwood communities, while usually dominated by *B. pubescens* ssp. *odorata* also contain additional taxa, including in particular, *Ilex aquifolium, Sorbus aucuparia, Prunus padus, Salix cinerea* and *Lonicera periclymenum*. The field layer closely resembles the flora occurring within the predominant oak and birch woodland communities of south and west Scotland (Birks, H.J.B., 1973). A

Table 2 - Characters that identify *Betula pendula* and *B. pubescens*

	B. pendula	*B. pubescens* ssp. *pubsecens*	*B. pubescens* ssp. *odorata*
Habit	Tree; single stem up to 30m	Tree; single stem 5-20m	Tree or shrub; 1 - several stems 1-12m
Bark	Silvery; black and fissured at base	Brown or grey but not different at base	
Branches	Pendulous	Never pendulous	Sometimes pendulous
Twigs	Glabrous with resin glands	Pubescent without resin glands	Sparsely pubescent often with resin glands
Leaves	2-7cm; sub-glabrous; acuminate; sharply biserrate	2-5.5cm; pubescent; acute; coarsely biserrate	1.5-4cm; slightly pubescent
Buds	Not viscid	Not viscid	Viscid
Pollen	20µm	23µm	26µm
Fruit	Wing 2-3x width of nutlet; nutlet glabrous; upper edge of wing surpassing stigmas	Wing 1.5x width of nutlet; nutlet pubescent at apex; upper edge of wing not surpassing stigmas	Wing as broad as nutlet
2n	28	56	56
Habitat	Tolerant of dry conditions	More tolerant of wet and cold conditions	

Source: *Personal communication*, Dr Edward Lodge, University of London (1978) further similarity with western deciduous woodland communities is the luxuriant development of bryophytes and lichens upon tree bark and rock surfaces.

DERIVED PLANT COMMUNITIES

Characteristic acid grassland and dwarf shrub heath communities often develop in areas where tree cover has been lost through felling, and where significant grazing or episodic burning follows thereafter. Limited areas within the Morar Basin, while devoid of tree cover, exhibit a species-poor variant of *Agrostis-Festuca* grassland, particularly on well-drained slopes, shallow soils and alluvium. The *Agrostis-Festucetum, sensu* McVean and Ratcliffe (1962) is dominated by the taxa *Agrostis capillaris* and *Festuca ovina*, with the constant species *Agrostis canina, Anthoxanthum odoratum, Galium saxatile* and *Potentilla erecta.*

The clear felling of woodland followed by grazing and periodic burning often results in the formation of a derived *Calluna vulgaris* heath. The *Callunetum vulgaris, sensu* McVean and Ratcliffe (1962) forms an extensive cover in favourable situations in the Morar Basin, particularly upon well-drained humus and podsols, within an altitudinal range from sea-level to approximately 450 metres OD. The *Callunetum* heath is dominated by *Calluna vulgaris, Erica cinerea* and *Potentilla erecta*, with the constant species *Agrostis cappillaris* and *Carex binervis.*

THE PHYTOSOCIOLOGY OF THE MIXED OAK AND BIRCH, AND BIRCH COMMUNITIES

The vegetation of the majority of mixed oak and birch, and birch woodland in the Scottish Highlands may be assigned to either one of two phytosociological *noda*, *sensu* McVean and Ratcliffe (1962). Although these noda grade into each other to a certain extent, they embrace a floristic range which is too wide to permit the definition of separate facies (McVean and Ratcliffe, 1962). The features of these noda are described below.

(1) *VACCINIUM*-RICH BIRCHWOOD (*Betuletum Oxaleto-Vaccinetum* nodum)

The *Vaccinium*-rich birchwood nodum comprises *Betula pubescens* and *Quercus petraea* along with the following constants: *Sorbus aucuparia, Blechnum spicant, Vaccinium myrtillus, Deschampsia flexuosa, Galium saxatile, Oxalis acetosella, Potentilla erecta, Hylocomium splendens, Pleurozium schreberi* and *Thuidium tamariscinum.* The field layer is often dominated by *Vaccinium myrtillus, Luzula sylvatica, Hyolcomium splendens* or *Thuidium tamariscinum. Blechnum spicant,* *Pteridium aquilinum, Vaccinium vitis-idaea, Agrostis capillaris, Anthoxanthum odoratum, Rhytidiadelphus loreus* and *Ptilium crista-castrensis* may attain co-dominance.

A shrub layer is usually represented by *Corylus avellana* along with *Lonicera perclymenum*; which is exclusive to this nodum. *Juniperus communis* is generally rare, however, it may become locally dominant in some situations.

Species of oak, either *Quercus petraea* or *Q. robur*, often succeed *Betula pubescens* and become the dominant tree, up to an altitude of approximately 275 metres in the southern and east-central Highlands, and up to an altitude of approximately 150 metres in the west of Scotland. Furthermore, there is either little or no accompanying change in the associated field layer. Most of the Highland oakwoods may be referred to this nodum. *Sorbus aucuparia* is often common within the tree canopy, and may become co-dominant or dominant in places (Anderson, 1950; McVean, 1958).

Birch is a natural pioneer tree species, and therefore does not form a climax forest or woodland. The principal woodland trees which generally follow birch in the natural pattern of succession are pine and oak. However, these currently appear to be largely unable to succeed birch and form natural climax woodland at many sites in Scotland; a possible factor is the extensive loss of viable populations of pine and oak trees from vast areas of the Highland landscape. Paradoxically, birch is a prolific seed producer which benefits from wind dispersal and transport of both pollen and fertile seeds. Furthermore, it appears to regenerate more freely than any of the other native trees in Scotland. Extensive areas of pioneer birchwood may be observed, colonizing open moorland and grassland areas in many places, particularly on Deeside, in the eastern Highlands of Scotland.

The *Betuletum Oxaleto-Vaccinetum* nodum may be distinguished from the closely related native Scots pine associations by the presence of many taxa, including *Corylus avellana, Lonicera periclymenum, Rubus idaeus, Hyacinthoides non-scripta, Luzula sylvatica, Viola riviniana, Thuidium tamariscinum*, and by the absence of *Goodyera repens*.

(2) HERB-RICH BIRCH AND OAKWOOD (*Betula*-herb nodum)

The herb-rich birch and oakwood nodum comprises *Betula pubescens* and *Quercus petraea* along with the following constants: *Blechnum spicant, Anthoxanthum odoratum, Galium hercynicum, Oxalis acetosella, Potentilla erecta, Viola riviniana* and *Hylocomium splendens*. Possible dominant species are *Oreopteris limbosperma, Agrostis tenuis, Anthoxanthum odoratum, Hylocomium splendens* and *Thuidium tamariscinum*. Although members of the Gramineae are often the most prominent plants, this nodum also includes communities which are rich in alkaliphilous herbaceous taxa.

Tall shrubs are usually less common compared with the *Vaccinium*-rich birchwood, however, this appears to be entirely attributable to the intensity of grazing and browsing activity which the woodland is subjected to during the year, by both wild herbivores and domesticated livestock. This nodum is common to birchwoods and also to the floristically poor stands of oak which typify many Highland oakwoods; it is distinguished from the *Betuletum Oxaleto-Vaccinium* nodum by the virtual absence of *Vaccinium* spp. and by the appearance, or increase in abundance of the following taxa: *Holcus lanatus, Hyacinthoides non-scripta, Anemone nemorosa, Conopodium majus, Lysimachia nemorum, Primula vulgaris, Ranunculus ficaria, R. repens, Viola riviniana, Mnium hornum, M. undulatum, Thuidium tamariscinum* and *Plagiochila asplenioides.*

Both birchwood noda occur throughout the Scottish Highlands, within an altitudinal range from sea-level up to approximately 610 metres OD. The soils which develop beneath these noda are typically leached brown earths or truncated posdols, although they are not as markedly podsolized as those occurring within the Scots pinewood communities. The *Betuletum Oxaleto-Vaccinetum* nodum tends to occur upon black, mildy acidic humus which has a well developed soil crumb structure. The soil profile may also reveal a shallow A_2 horizon, in many cases, however, the humus rests directly upon bedrock. In contrast, the *Betula*-herb nodum often tends to occur upon brown mineral soil with mull humus, and a B horizon consisting of deep red-brown sand and stony loam.

The broad-leaved deciduous woodland cover of the Morar Basin exhibits a heterogeneous floristic composition which may be assigned to both the *Betuletum Oxaleto-Vaccinetum* and *Betula*-herb noda *sensu* McVean and Ratcliffe (1962).

The definition of phytosociological noda based upon the composition of woodland field layers is often difficult because a range of constant taxa often exhibit an erratic distribution spatial distribution and frequency.

SCOTS PINE WOODLAND COMMUNITIES

The island archipelago situated in the western part of Loch Morar, at longitude 5°47'W by latitude 56°58'N, is dominated by impressive stands of Scots pine, *Pinus sylvestris* var. *scotica* This site is exceptional within the Morar Basin because it presents a significant variation in floristic composition within the zone of predominant broad-leaved woodland cover which characterizes western Scotland.

A map of the principal islands of the Morar archipelago is illustrated in Figure 6. The total area of the archipelago is approximately 22.3 hectares. The area of the individual islands is listed in Table 3, which the author computed using a method of proportional squares and a copy of the bathymetrical survey chart of the Morar Basin by Murray and Pullar (1910, Plate XLIII).

A view of the Morar archipelago looking southeast from Torr na Ba, North Morar, is illustrated in Plate 5. In the centre of this view is Eilean Ban, situated at longitude *circa* 5°47'17"W, while to the far left is Eilean a'Meadhoin. Other small isles appear beyond, with the hills of South Morar in the background.

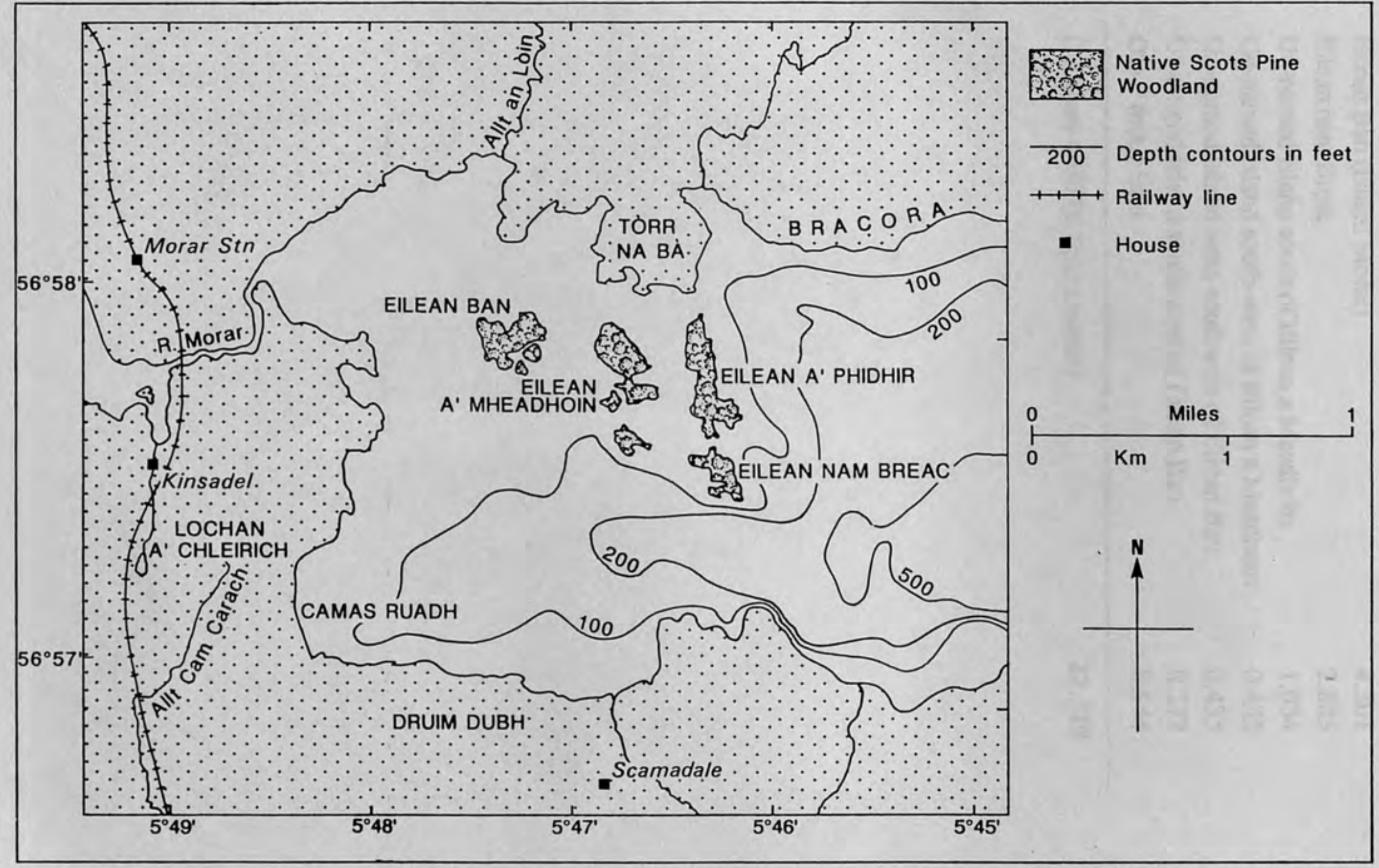
The floristic composition and phytosociology of the Scots pine woodland of the Morar archipelago was investigated by the author to ascertain whether these stands of trees represent quasi-natural Scots pine woodland. This investigation involved a review of the literature pertaining to the geographical distribution, floristic composition, phytosociology, age-structure and dynamics of Scots pine woodland in Scotland (Steven and Carlisle, 1959; McVean and Ratcliffe, 1962; Birks, H.J.B., 1977). Brief descriptions of the Scots pine woodland occurring on Eilean a'Phidhir and Eilean a Meadhoin in the Morar archipelago (McVean, 1958; Rose, 1977b, 1977c) also provided additional data. The author also investigated the stands of Scots pine on Eilean Ban in the Morar archipelago and assessed the phytosociology of the woodland cover *sensu* McVean and Ratcliffe (1962).

The native Scots pine woodland of the Scottish Highlands is the most localized of all the major British woodland communites. In this region, *Pinus sylvestris* var. *scotica* locally replaces *Quercus petraea* and *Q. robur* as the dominant woodland tree.

The Scots pine communities of the Scottish Highlands as a whole, represent a southern and western outlier of the Boreal Coniferous Forest vegetation of northern Europe (Tansley, 1949). *Pinus sylvestris* is a tree which can grow up to 30 metres in height. Furthermore, it is the sole representative of the family Pinaceae and Genus *Pinus* which is native to the British Isles. The geographical distribution of the tree is Eurasian, extending from Scotland and north-west Spain in the west, to the Pacific coast of north-east Asia in the east, and from southern Spain in the south, to northern Norway in the north (Steven and Carlisle, 1959; Mirov, 1967). The entire European distribution of *Pinus sylvestris* is recorded on maps (Jalas and Suominen, 1973) and the north-west European distribution has been described in the literature (Fitter, 1978).

A detailed review of the native Scots pine woodland of Scotland by Steven and Carlisle (1959) provides descriptions and geographical maps of the majority of surviving areas of native Scots pine in Scotland.

Fig.6 THE ARCHIPELAGO OF LOCH MORAR

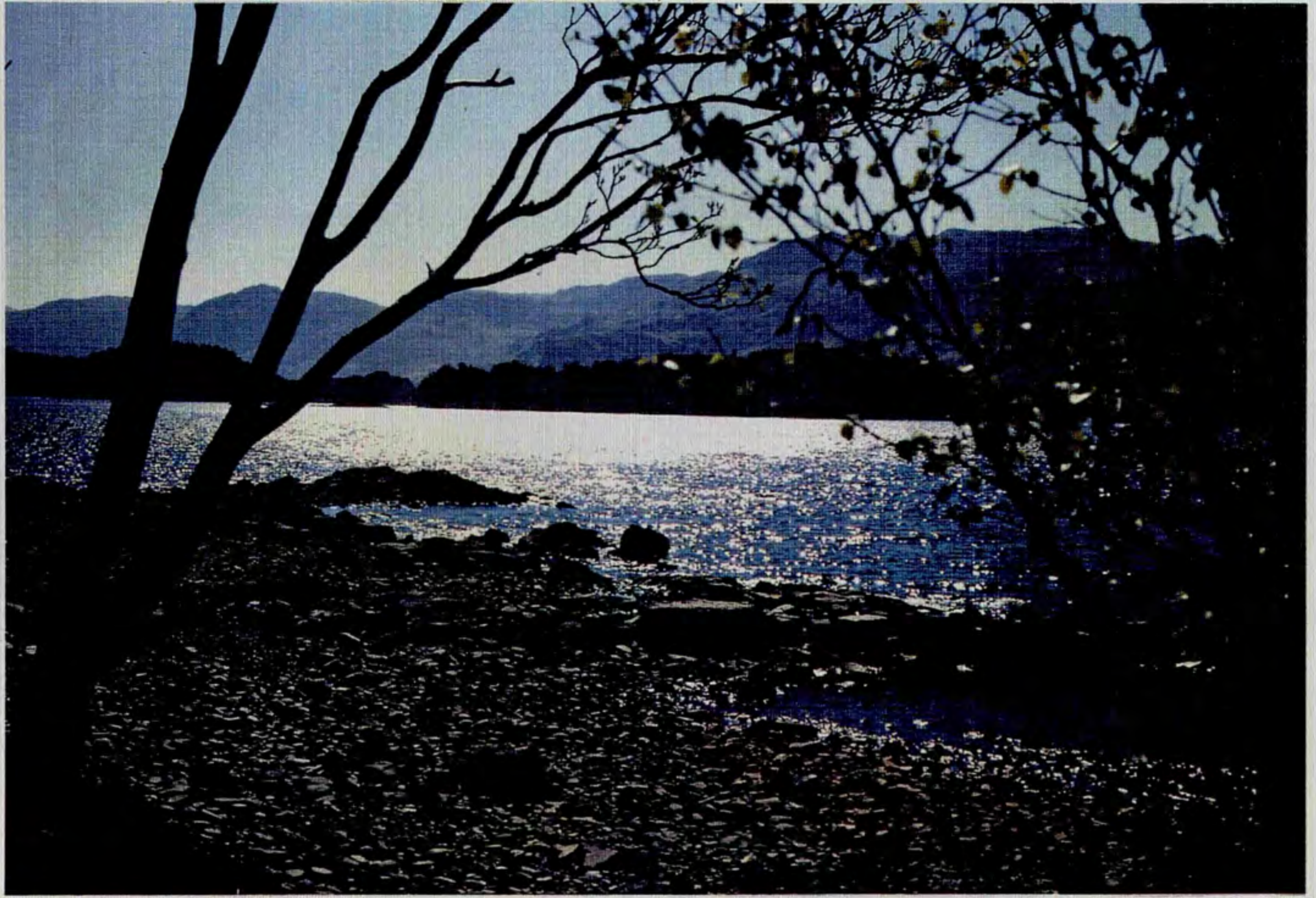


Source: Murray and Pullar (1910)

Table 3 - The area of the islands which comprise the Morar archipelago

Island	*Area (hectares)*
Eilean a'Phidhir	6.860
Eilean a Meadhoin	5.553
Eilean Ban (Island Morar)	4.301
Eilean nam Breac	2.885
Un-named island south of Eilean a Meadhoin	1.034
Un-named island south-west of Eilean a Meadhoin	0.435
Un-named island west-southwest of Eilean Ban	0.435
Un-named island south-west of Eilean Ban	0.272
Other rocky isles	0.544
[1 hectare = 10,000 square metres]	22.319

Plate 5 The Morar archipelago, looking south-east from Torr na Ba, North Morar



GEOGRAPHICAL DISTRIBUTION OF SCOTS PINE IN SCOTLAND

Within Scotland, native Scots pine has been recorded between latitude 57°57'N to 56°22'N, from a northern limit at Glen Einig in Ross and Cromarty, to a southern limit at Glen Falloch in Perthshire, and between longitude 2°53'W to 5°38'W, from an eastern limit at Glentanar in Aberdeenshire, to a western limit at Shieldaig in Wester Ross (Steven and Carlisle, 1959).

The altitudinal range of the native Scots pine in Scotland is from near sea-level at Shieldaig in Wester Ross, and Barisdale in Knoydart, north-west Highlands, to an upper altitudinal limit for Scots pine in Scotland, at approximately 640 metres OD on a mountain slope at Creag Fhiachlach, Cairngorm district, in the east Central Highlands.

The most extensive area of surviving native Scots pine woodland occurs around Rothiemurchus and Abernethy, Speyside, in the east Central Highlands. This represents one of the largest areas of continuous quasi-natural woodland now remaining in the British Isles.

While native Scots pine woodland communities are generally considered to be local to the Scottish Highlands, the possibility also exists that some communities of *Pinus sylvestris* which occur on acid lowland mires, and southern heaths in Britain, may represent fragmentary remanent populations (Ratcliffe, 1977). The geographical distribution of native Scots pine woodland in Scotland is illustrated in Figure 7. Steven and Carlisle (1959) identified eight main geographical groups of native Scots pine woodland distributed among thirty-five locations in Scotland, which are cited in Table 4. The close proximity of Loch Morar to the Scots pinewood at Barisdale in the Great Glen group is indicated in Figure 7.

THE FLORISTIC COMPOSITION OF SCOTS PINE WOODLAND COMMUNITIES

Native Scots pine woodland communities exhibit a distinct floristic variation between different geographical regions in Scotland. This variation is clearly evident between western and eastern regions, despite the impact of extensive deforestation, and recent afforestation programmes.

Native Scots pine communities are often developed on north-facing slopes, upon substrata which consist predominantly of coarse sand and gravel, with soil profiles which are often strongly podsolized. In eastern Scotland, the tree layer is generally dominated by *Pinus sylvestris*, which forms dense stands. *Betula* spp. and *Sorbus aucuparia* often occur freely within the tree layer. In the Central Highlands, *Quercus petraea* is also occasional in sheltered situations, generally at low altitude and with a southerly aspect. The shrub layer and field layers are often poorly developed or absent in conditions of dense shade. However, where the tree canopy is relatively open, the shrub *Juniperus communis* is often abundant.

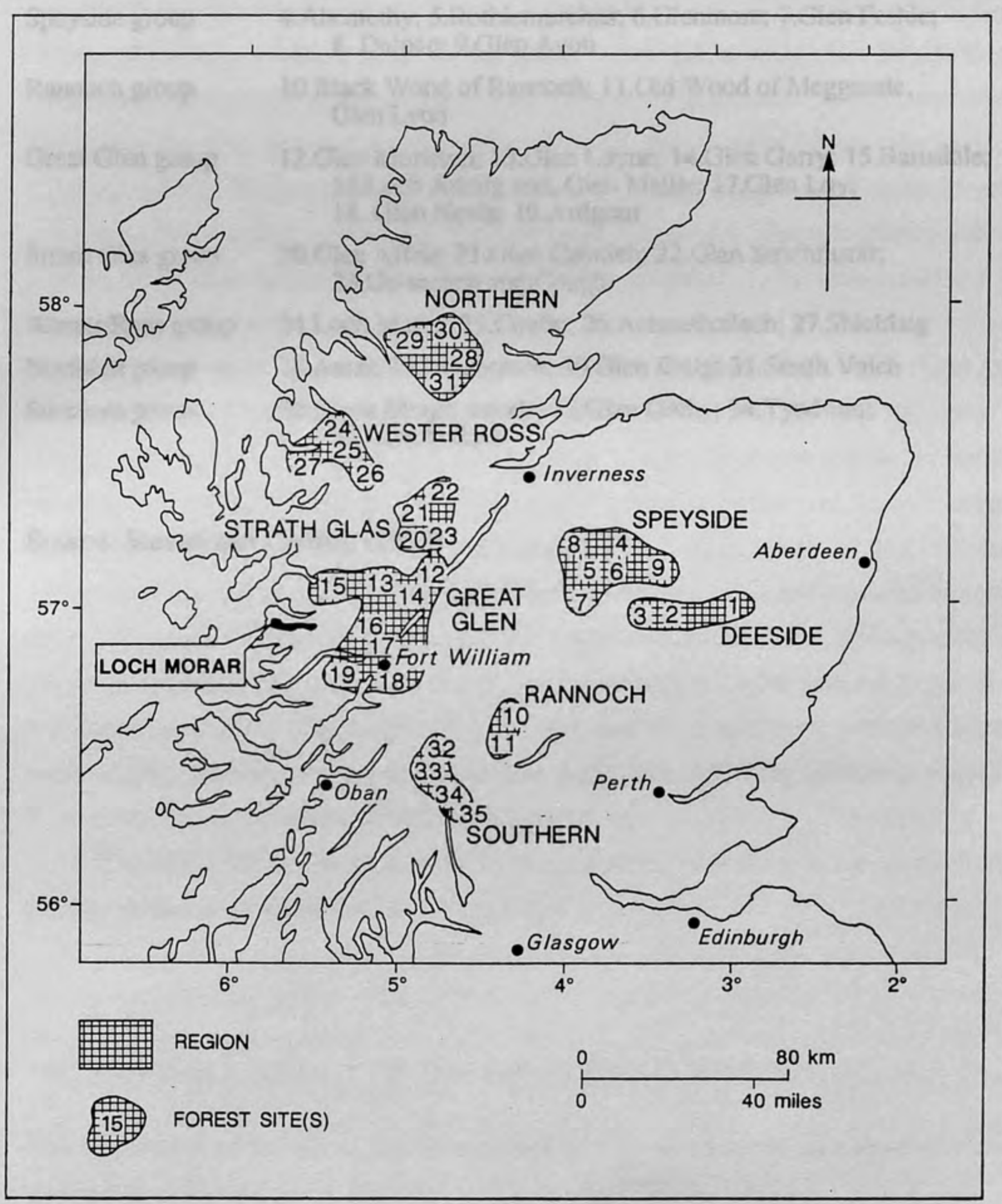
In western Scotland, Scots pine woodland generally exhibits a wider range of deciduous tree species within the tree layer, including *Betula pubescens, Sorbus aucuparia, Populus tremula, Ilex aquifolium* and *Prunus padus. Alnus glutinosa* often grows on damp ground and stream margins within these communities. The shrub *Juniperus communis* is generally uncommon, in contrast to its abundance in eastern regions. Tall individuals of *Calluna vulgaris* and *Vaccinium myrtillus* are generally common beneath relatively open areas in the tree canopy, throughout the geographical distribution range of native Scots pine in Scotland.

The field layer of Scots pine communities exhibits a distinctive and characteristic assemblage of plants. The taxa *Deschampsia flexuosa, Melampyrum pratense* and *Lathyrus montanus* are generally constant, while a diagnostic northern element is widely represented by *Pyrola minor, Listera cordata, Trientalis europaea, Goodyera repens* and the bryophyte *Ptilium crista-castrensis.* Local northern taxa include *Linnaea borealis, Orthilia secunda, Pyrola media* and *Moneses uniflora. Teucrium scorodonia,* which is common in Highland oakwoods, occurs occasionally in western Scots pinewoods at low altitude. *Pteridium aquilinum* is often abundant in western pinewoods, but less frequent in eastern regions. Other pteridophytes which may be locally abundant include the taxa *Blechnum spicant* and *Oreopteris limbosperma.*

Some plants of the field layer appear to be uniquely associated with native Scots pine tree cover, the include *Moneses uniflora* which is very rare, and *Goodyera repens* which occurs locally and forms mycorrhizal and saprophytic associations with the root system of native *Pinus sylvestris* trees. Indeed, these taxa may represent potential indicators of ecological continuity of tree cover at sites of native Scots pine woodland. The possibility exists, however, that these taxa may be conveyed, along with Scots pine seedlings, from sites of native pinewood which subsequently develop in the field layer of recent plantations (Ratcliffe, 1977).

The field layer increases in diversity with the addition of various upland, sub-montane and montane species, especially where the woodland merges with moorland, where pine and oak communities converge as the upper altitudinal limits of plant communities become depressed across north-western Scotland, or where the pine community is interrupted by other habitats, including streams and rock outcrops. The field layer may correspondingly exhibit a range of taxa which generally occur on soils and peat, including *Rubus chamaemorus, Empetrum nigrum* ssp. *hermaphroditum, Cornus suecica, Lycopodium clavatum,*

Fig.7 GEOGRAPHICAL DISTRIBUTION OF NATIVE SCOTS PINE WOODLAND IN SCOTLAND



Source: Steven & Carlisle (1959); Pears (1985)

Table 4 - The principal sites of native Scots pine woodland in Scotland

Geographical Group	*Location*
Deeside group	1.Glentanar; 2.Ballochbuie; 3.Mar
Speyside group	4.Abernethy; 5.Rothiemurchus; 6.Glenmore; 7.Glen Feshie; 8. Dulnan; 9.Glen Avon
Rannoch group	10.Black Wood of Rannoch; 11.Old Wood of Meggernie, Glen Lyon
Great Glen group	12.Glen Moriston; 13.Glen Loyne; 14.Glen Garry; 15.Barisdale; 16.Loch Arkaig and, Glen Mallie; 17.Glen Loy; 18. Glen Nevis; 19.Ardgour
Strath Glas group	20.Glen Affric; 21.Glen Cannich; 22.Glen Strathfarrar; 23.Guisachen and Cougie
Wester Ross group	24.Loch Maree; 25.Coulin; 26.Achnashellach; 27.Shieldaig
Northern group	28.Amat; 29.Rhidorroch; 30.Glen Einig; 31.Strath Vaich
Southern group	32.Black Mount woods; 33.Glen Orchy; 34.Tyndrum; 35.Glen Falloch

Source: Steven and Carlisle (1959)

L. annotinum, Huperzia selago and *Diphasiastrum alpinum.* Streamside alluvium is often colonized by *Alchemilla alpina*, while basic rocks and flushes provide habitats for *Saxifraga oppositifolia, S. aizoides, Tofieldia pusilla, Parnassia palustris, Melica nutans, Sanicula europaea, Gentianella amarella* and *Juncus alpinoarticulatus.*

The ground layer within the native Scottish pinewoods is generally well developed and often luxuriant with bryophytes and lichens. A common assemblage of bryophyte taxa which exhibit a widespread distribution within the British Isles includes *Hylocomium splendens* and *Plagiothecium undulatum*, which are often dominant in the ground layer, accompanied by *Campylopus flexuosus, C. pyriformis, Dicranum scoparium, Hypnum cupressiforme, Leucobryum glaucum, Pleurozium schreberi, Polytrichum formosum, Pseudoscleropodium purum, Thuidium tamariscinum, Diplophyllum albicans, Lepidozia reptans* and *Lophocolea bidentata.*

Polytrichum formosum is often abundant in damp situations. In northern and western regions *Rhytidiadelphus triquetrus* and *R. squarrosus* are also common in the ground layer. A group of bryophyte taxa which are characteristic of native pinewood throughout the Scottish Highlands includes *Hylocomium splendens, H. brevirostre, Rhytidiadelphus loreus* and *Ptilium crista-castrensis.* The majority of bryalean taxa, with the exception of *Polytrichum commune*, are replaced to some extent in areas of impeded drainage by representatives of the Sphagnales, in particular *Sphagnum palustre* and *S. quinquefarium.* The ground layer also exhibits a variety of lichens growing on soil, leaf litter and rock surfaces, along with taxa which are common in heaths and grassland, including *Cladonia gracilis, C. portentosa, C. pyxidata and C. rangiformis.*

The epiphytic (corticolous) lichen communities occurring in the native Scots pine woodlands are described in Chapter 4.

THE PHYTOSOCIOLOGY OF THE SCOTS PINE COMMUNITIES

The vegetation of the Scots pine communities may be assigned to one of two well defined associations *sensu* McVean and Ratcliffe (1962).

(1) PINEWOOD *VACCINIUM*-MOSS ASSOCIATION (*Pinetum Hylocomieto-Vaccinetum*)

This association is characteristic of moderately dense stands of Scots pine occurring throughout the Central and Northern Highlands. Furthermore, it is also frequently developed within Scots pine plantations. This association consists of *Pinus sylvestris* along with *Calluna vulgaris, Vaccinium myrtillus, V. vitis-idaea* and *Hylocomium splendens.* The ground layer may be dominated by *Vaccinium myrtillus, V. vitis-idaea, Hylocomium splendens* or *Rhytidiadelphus triquetrus.* However, *Deschampsia flexuosa* and *Ptilium crista-castrensis* may occasionally attain co-dominance with the dwarf shrubs and bryophytes. Although tall shrubs are usually absent from this association, moribund individuals of *Juniperus communis* may occur occasionally. *Betula pubescens* and *Sorbus aucuparia* often form a distinctive element within the tree canopy, and their seedlings are frequent in the field and ground layers. The taxon *Goodyera repens* is exclusive to the association, although it may also occur on tussocks in the alternative *Pinetum Vaccinetum-Callunetum* assocation. McVean and Ratcliffe (1962) identified two facies of the *Pinetum Hylocomieto-Vaccinetum,* which generally occur together within a Scots pine community:

(a) The *myrtillosum* facies, which is dominated by *Vaccinium* spp. occurs typically beneath a tree canopy of average density.

(b) The *triquetrosum* facies, which is dominated by *Hylocomium splendens* or *Rhytidiadelphus triquetrus,* occurs in situations where the tree canopy is particularly close or where it has been close during the past.

The *Pinetum Hylocomieto-Vaccinetum* association occurs within an altitudinal range from sea level to over 475 metres OD, currently forming extensive areas of native woodland and plantation in eastern Scotland, while only forming localized communities in western Scotland.

In situations where felled Scots pine trees have been succeeded by birch, there may be a gradual transition to either of the birchwood noda (*Betuletum Oxaleto-Vaccinetum* or *Betula*-herb noda) or to the *Pinetum Vaccineto-Callunetum* association; the latter occurs especially where the loss of pine trees is accompanied by the exclusion of grazing animals from the woodland site. The *Pinetum Hylocomieto-Vaccinetum* association appears to be comparable with the European *Pineto-Vaccinenetum myrtilli* association *sensu* Braun-Blanquet, Sissingh and Vlieger (1939). The soils which develop beneath both Scots pine associations generally comprise raw mor humus overlying well-drained sand and gravel. The soil profile is characterized by a well developed podsol in both cases.

(2) PINEWOOD *VACCINNIUM-CALLUNA* ASSOCIATION (*Pinetum Vaccineto-Callunetum)*

This association is characteristic of relatively open pinewood, mixed pine and birch wood, and pure stands of birch which have recently colonized ground formerly occupied by Scots pine woodland. This association consists of *Pinus sylvestris* along with *Calluna vulgaris, Vaccinium myrtillus, V.vitis-idaea, Deschampsia flexuosa, Hylocomium splendens, Plagiothecium undulatum* and *Ptilium crista-castrensis.* The tree canopy often contains a variety of trees, including *Ilex aquifolium* which is a common feature of this association in western Scotland. *Juniperus communis* is a characteristic tall shrub, which may be abundant at certain sites in the central and eastern Highlands. *Calluna vulgaris, Vaccinium myrtillus, Hylocomium splendens, Ptilium crista-castrensis* and *Sphagnum* spp., may all become dominant in their respective layers within the woodland community. This association is distinguished from the *Pinetum Hylocomieto-Vaccinetum* association by the presence of the liverworts *Aulacomnium palustre* and *Calypogeia trichomanis.*

The *Pinetum Vaccineto-Callunetum* association is co-extensive with that of native Scots pinewood in Scotland, while it is generally absent from plantations of Scots pine, where the tree canopy is usually dense. This association occurs within an altitudinal range from sea-level to almost 305 metres OD in western Scotland, and from approximately 275 metres to 610 metres OD in the eastern Highlands, where it tends to replace the *Pinetum Hylocomieto-Vaccinetum* association with increasing altitude.

The majority of stands occur on damp north-facing slopes. Furthermore, this association is apparently uniquely independent of the trees. In many cases it can survive the total loss of the tree cover provided that the soil remains sufficiently wet that it is not converted to *Calluna vulgaris* heath by rotational burning.

THE AGE-STRUCTURE AND DYNAMICS OF THE SCOTS PINE COMMUNITIES

Available evidence indicates that during the past where native Scots pine formed natural climax forest in Scotland, the stands of trees exhibited a mosaic of segregated age-classes of individual trees. This pattern of development contrasts markedly with the alternative mixed-age composition of other natural forest stands, which follow a classic cycle of regeneration and maturity within the spaces created by the death of parent trees.

Three main types of age-structure are currently distinguishable among the stands of native Scots pine occurring in Scotland (McVean and Ratcliffe, 1962).

(1) QUASI EVEN-AGED STANDS OF 80-150 YEARS

These stands often exhibit an apparent age-diversity and a range of different tree crown forms associated with dominant and supressed trees. Although the woodland vegetation may be assigned to either one of the two main Scots pinewood associations *sensu* McVean and Ratcliffe (1962), the *Pinetum Hylocomieto-Vaccinetum* association appears to be most frequently represented. Although pine seedlings in the first and second year of growth are often common, tree regeneration is extremely limited within deep moss or accumulations of undecomposed pine leaf litter in the ground layer, which may desiccate during dry spring months. Advanced growth of pine saplings is generally rare, although some cases are recorded from the east central Highlands. The quasi even-aged stands appear to result from a phase of mass regeneration following a period of fire within the Scots pine community.

(2) STANDS WITH A TWO-GENERATION STRUCTURE

These stands comprise a matrix of pioneer Scots pine trees of between 150 to 200 years of age, surrounded by upright progeny of between 80 to 100 years of age. The vegetation is typically a mixture of both Scots pinewood associations *sensu* McVean and Ratcliffe (1962), which may be in an intermediate stage of development.

Although tree regeneration is uncommon within older stands, some local regeneration may occur in the vicinity of the parent trees, particularly in situations where grazing animals are excluded and fire is prevented. The formation of dense thickets of Scots pine surrounding parent trees is typical. Indeed, at Abernethy Forest, Speyside, young mixed-age Scots pinewood near Loch Garten exhibits features of advanced growth of pine saplings, with a diverse shrub layer comprising *Juniperus communis, Betula* and *Sorbus aucuparia*, and a field layer comprising a number of herbaceous taxa, which are typically associated with mull humus formation, including *Viola riviana* and *Oxalis acetosella.* Dense thickets of younger Scots pine trees have also developed within the vicinity of the parent trees, along with self-thinning of some thickets and the death of parent trees. Furthermore, active colonization by Scots pine and regeneration at all stages is recorded on an adjacent area of enclosed heather moor, which has remained unburnt for some years (McVean and Ratcliffe, 1962).

(3) PINE HEATHS

Tree cover is variable in extent within Scots pine heaths. The individual trees are generally between 150 to 200 years of age and typically exhibit spreading crowns. The vegetation may be assigned either to the *Pinetum Vaccineto-Callunetum* association or to the non-woodland *Callunetum vulgaris* association, in situations where heath burning has occurred within open stands of Scots pine trees.

Regeneration of Scots pine trees is generally uncommon in pine heaths, principally because pine seedling growth occurs slowly within accumulations of deep moss and the cover of dwarf shrubs. Regeneration is also hindered by damage incurred from browsing deer during the winter and spring, consequently any emergent pine seedlings rarely grow above 15 centimetres in height. The possibility exists that open stands of Scots pine might become successfully established in these situations, if herbivorous animals are excluded.

The extent to which native Scots pine communities in Scotland have been dependent upon fire for their perpetuation remains unknown. However, it is clear that edaphic conditions beneath *Pinus sylvestris* communities in Scandinavia eventually become unsuitable for pine tree regeneration because the mor humus ceases to be biologically active. Fire generally restores biological activity and enables regeneration to take place (Tamm, 1950). The effect of anthropogenic influence, through the selection and segregation of mor humus forming species, may also be implicated in this phenomenon of biological stagnation. The floristic composition of the climax Scots pine vegetation during the past may have included both mull and mor humus forming taxa, along with a proportion of deciduous trees and associated mull humus forming herbaceous taxa (Handley, 1954).

All areas of dense Scots pine regeneration in Scotland appear to result from the colonization of heather moor by pine seedlings, after an episode of fire. Although the development of the pine seedlings proceeds slowly at first, it gradually increases and eventually becomes vigorous enough to surpass the developing *Calluna vulgaris*. The emergent pine seedling can tolerate moderate browsing and these develop into dense thickets. Eventually, a quasi even-aged stand of Scots pine trees arises. The deep shade cast by these stands eventually causes the elimination of the *Calluna* heather. Where the initial number of pine seeds is insufficient to produce dense thickets, an open pine-heath develops instead.

Paradoxically, the episode of fire which initially encouraged *en masse* regeneration of Scots pine, ultimately prevents the continuation of the regenerative process, by indirectly promoting conditions, e.g. deep shade, which are unfavourable for the development of subsequent seedling generations. Regeneration occurs locally in the Scots pinewoods of Speyside and Deeside in the east central Highlands, while elsewhere in Scotland, regeneration is either poor or absent (McVean and Ratcliffe, 1962). Natural regeneration is currently limited in many sites, particularly in western Scotland, probably due to a combination of factors, including high relative humidity, unfavourable soil conditions, in particular acid mor humus and browsing by indigenous red deer (Birks, H.H., 1972a).

SCOTS PINE WOODLAND COMMUNITIES ON THE MORAR ARCHIPELAGO

The principal islands of the Morar archipelago are dominated by impressive stands of *Pinus sylvestris* trees. A view of these stands is illustrated in Plate 6, which was kindly provided by Dr David Shirt, University of London. These islands collectively cover an area of approximately 22 hectares, and range in altitude between 10 and 39 metres OD. The smaller rocky isles associated with the archipelago are frequently inundated during storms and therefore typically support only a pioneer phase of woodland. The archipelago has been designated as a Grade 1 woodland site by the Nature Conservancy Council (Ratcliffe, 1977). These islands exhibit woodland communities containing rare species and physiognomic features, including well developed scrub layers dominated by *Corylus avellana* (designated as Grade 2 by the Nature Conservancy Council), which are significant at a national level.

A floristic survey of Scots pine woodland on Eilean Ban, Loch Morar is presented in Table 5. This survey was jointly executed by the author and Angela Newton BSc (Honours), University of London.

The stands of Scots pine on the Morar archipelago exhibit a two-generation age-structure, with scattered pioneer trees estimated to be 150-200 years of age, with characteristic spreading crowns, surrounded by a matrix of younger progeny comprising tall upright trees estimated to be 80-100 years of age, along with stands

Plate 6 Native Scots Pine woodland on the Morar archipelago, Loch Morar

Table 5 - Floristic survey of Scots pine woodland on Eilean Ban, Loch Morar (Latitude 56°57'55"N, Longitude 5°47'17"W, altitudinal range 10-30 metres OD, area 4.30 hectares)

	Phytosociological category (*sensu* McVean and Ratcliffe, 1962)		
Taxon	P-H-V*	P-V-C*	B-O-V*
Pinus sylvestris var *scotica*	C	C	
Betula pubescens spp. *odorata*			C
Sorbus aucuparia			C
Ilex aquifolium			
Corylus avellana			
Salix spp.			
Viburnum opulus			
Taxus baccata			
Calluna vulgaris	C	C	
Vaccinium myrtillus		C	C
Luzula sylvatica			
Deschampsia flexuosa		C	C
Juncus spp.			
Hyacinthoides non-scripta			
Lonicera periclymenum			
Lotus corniculatus			
Potentilla erecta			C
Primula vulgaris			
Oxalis acetosella			C
Viola riviniana			
Blechnum spicant			C
Polypodium vulgare			
Pteridium aquilinum			
Dicranum scoparium	C	C	
Hylocomium splendens	C		C
Hypnum cupressiforme			
Hypnum cupressiforme var. *filiforme*			
Polytrichum formosum			
Pseudoscleropodium purum			
Rhytidiadelphus triquetrus			
Sphagnum spp.			
Thuidium tamariscinum			C

* P-V-C - *Pinetum Vaccineto Callunetum*
P-H-V - *Pinetum Hylocomieto Vaccinetum*
B-O-V - *Betuleum Oxaleto Vaccinetum*
C - constant species

of trees estimated to be 40-80 years, e.g. at the northern end of Eilean a'Phidhir (McVean, 1958). This age-structure is a typical feature of many native Scots pine communities in Scotland (McVean and Ratcliffe, 1962).

The Scots pine community on Eilean Ban also exhibits at least eight constant species which occur in the *Betuletum Oxaleto-Vaccinetum* (*Vaccinetum*-rich birchwood) *sensu* McVean and Ratcliffe (1962). These constants are *Betula pubescens* ssp. *odorata, Sorbus aucuparia, Vaccinium myrtillus, Blechnum spicant, Deschampsia flexuosa, Potentilla erecta, Oxalis acetosella, Hylocomium splendens* and *Thuidium tamariscinum.* The liane *Lonicera periclymenum,* which is exclusive to this nodum, is also present on this island. Furthermore, the field layer is often locally dominated by taxa, including *Viola riviniana, Oxalis acetosella* and *Primula vulgaris,* which are typically associated with mull humus.

In areas where senescent Scots pine trees have fallen through the tree layer the ground beneath is often locally dominated by *Pteridium aquilinum.* The presence of this taxon within the field layer is often attributable to the effect of fire within a woodland. Where the terrain is undulating and covered with boulder scree extensive mats of *Sphagnum* (ref. *quinquefarium*) communities have developed within wet hollows, while ground with improved drainage is often locally dominated by *Polytrichum formosum.* Hypnaceous bryophytes including *Hylocomium splendens, Hypnum cupressiforme, Rhytidiadelphus triquetrus* and *Dicranum scoparium* form extensive and luxuriant carpets on rock surfaces and around the bases of tree trunks. *Hylocomium splendens* is often locally dominant beneath *Pinus sylvestris.* The pteridophyte *Blechnum spicant*, along with characteristic Scots pine woodland taxa *Goodyera repens* and *Listera cordata* usually occur among these bryophytes.

The presence of isolated and stunted Scots pine trees among tall *Calluna vulgaris,* interspersed with deep accumulations of *Sphagnum* spp. on some islands in the archipelago, e.g. Eilean Phidhir (McVean, 1958) and Eilean Ban, suggests that a derivative community, defined as a *Callunetum vulgaris* association *sensu* McVean and Ratcliffe (1962) has developed in some areas, possibly following fire or tree clearance during the past.

The extistence of former settlements on the Morar archipelago is indicated by the remains of abandoned buildings. A small chapel ruin is situated on the northeastern part of Eilean Ban. An historical record which survives in Saint Columbs' church, near Beoraidmore, on the northern shore of Loch Morar, indicates that a seminary existed on Eilean Ban towards the end of the eighteenth century. On the nearby island of Eilean a'Phidhir, traces of old walls at the northeastern point of the island has been recorded (McVean, 1958). Furthermore, the tree canopy in this area also exhibits *Taxas baccata, Tilia cordata* and *Acer* *pseudoplatanus*. The latter two taxa may have been actively introduced during the settlement of the island. Evidence of fire and the burning of vegetation is also indicated by the presence of charcoal fragments at the base of leaf litter in soil profiles on Eilean a'Phidhir (McVean, 1958).

The Scots pine community on Eilean Ban exhibits at least five constant species which are common to both *Pinetum Hylocomieto-Vaccinetum* and *Pinetum Vaccineto-Callunetum* associations, respectively. These constants are *Pinus sylvestris, Calluna vulgaris, Vaccinium myrtillus, Hylocomium splendens* and *Dicranum scoparium*. Two characteristic taxa associated with native Scots pine woodland, *Listera cordata* and *Goodyera repens* also occur on the archipelago (Ratcliffe, 1977). The taxon *Goodyera repens* is exclusive to the *Pinetum Hylocomieto-Vaccinetum* association. This association evidently forms only localized communities in western Scotland (McVean and Ratcliffe, 1962).

The Scots pine community on Eilean Ban also exhibits *Deschampsia flexuosa*, which is a constant species in the *Pinetum Vaccineto-Callunetum*, along with *Ilex aquifolium* which is a characteristic element of this association in western Scotland (McVean and Ratcliffe, 1962).

The tree canopy on the islands is generally dominated by *Pinus sylvestris* var. *scotica*, although in some area *Betula pubescens* ssp. *odorata* is co-dominant. *Ilex aquifolium* and *Salix* spp. are abundant, and *Sorbus aucuparia* is generally frequent within the tree layer. *Taxus baccata* is also occasional on the islands. *Alnus glutinosa* occurs on wet ground where the stands of trees are relatively open. On Eilean a'Meadhoin, stands of very old *Pinus sylvestris* additionally exhibit *Populus tremula* (Rose, 1977b).

A distinctive subordinate layer of young broad-leaved deciduous trees, including *Quercus petraea*, is present where the tree canopy is relatively open. A well developed shrub layer of *Corylus avellana* and *Taxus baccata* are also characteristic, particularly within mixed-age stands of *Pinus sylvestris*. The tall shrub *Juniperus communis* was not recorded by the author on Eilean Ban. Indeed, no records of this taxon are indicated from the other islands, e.g. Eilean a'Phidhir and Eilean a'Meadhoin, in the Morar archipelago. *Juniperus communis* is also uncommon in other western Scots pinewood communities, e.g. Loch Maree woods, Ross-shire (Birks, H.H., 1972a).

The field layer exhibits *Listera cordata* and *Goodyera repens*, which are particularly characteristic of native Scots pine woodland communities in Scotland. Where the tree canopy is relatively open the ground is often dominated by tall *Calluna vulgaris* and *Vaccinium myrtillus*. Where moderate shade is cast the bryophyte taxa *Hylocomium splendens* and *Rhytidiadelphus triquetrus* are generally dominant.

Both facies of the *Pinetum Hylocomieto-Vaccinetum* association, i.e. *myrtillosum* and *triquetrosum* facies respectively, are represented on Eilean Ban. The presence of the *Betuletum Oxaleto-Vaccinetum* nodum on Eilean Ban is particularly significant. Indeed, there are recorded instances where felling of Scots pine trees within a *Pinetum Hylocomieto-Vaccinetum* association has often led to the subsequent colonization of the cleared ground by birch trees. Furthermore, this change is evidently accompanied by a transition to either of the two birchwood noda *sensu* McVean and Ratcliffe (1962), while in situations where grazing animals have been excluded a transition to the *Pinetum Vaccineto-Callunetum* association arises instead (McVean and Ratcliffe, 1962). The evidence from the floristic survey clearly suggests that tree felling has occurred on Eilean Ban during the past.

The presence of *Luzula sylvatica* and *Vaccinium myrtillus* in particular, within the field layer on Eilean Ban, suggests that the current vegetation is not subjected to intensive grazing. Nevertheless, browsed seedlings of *Ilex aquifolium* and *Sorbus aucuparia* are widespread. The browsing is probably attributable to indigenous Red deer which leave identifiable tracks on the islands (McVean, 1958). These animals evidently swim from the northern shore of the loch to the archipelago and reach the individual islands across fordable channels.

The existence of dense thickets of young Scots pine trees surrounding parent trees on the archipelago is indicative that natural regeneration of *Pinus sylvestris* is proceeding in some parts of the Scots pine woodland, which is highly significant, in view of the extremely limited natural regeneration of Scots pine in western Scotland.

The floristic survey of the woodland cover on the Morar archipelago has revealed the following points:-

(1) The Scots pine community exhibits a characteristic two-generation structure; scattered pioneer trees, with spreading crowns are surrounded by a matrix of younger progeny which are tall and straight. This age-structure is typically encountered within native Scots pine communities occurring elsewhere in Scotland (McVean and Ratcliffe, 1962).

(2) The dominant vegetation on the Morar archipelago is a mixture of the two native Scots pine associations *sensu* McVean and Ratcliffe (1962). The *Pinetum Hylocomieto-Vaccinetum* association and *Pinetum Vaccineto-Callunetum* association are both represented on Eilean Ban. Furthermore, both facies of the *Pinetum Hylocomieto-Vaccinetum* association, i.e. *myrtillosum* and *triquetrosum* facies, are also represented.

(3) The woodland cover on Eilean Ban also exhibits *Vaccinium*-rich birch woodland defined as the *Betuletum Oxaleto-Vaccinetum* nodum *sensu* McVean and Ratcliffe (1962).

(4) The presence of isolated and stunted Scots pine trees among tall *Calluna vulgaris* interspersed with deep accumulation of *Sphagnum* spp. suggests that a *Callunetum vulgaris* association *sensu* McVean and Ratcliffe (1962) has developed in some areas, possibly following fire or tree clearance during the past; charcoal fragments occur at the base of leaf litter in podsolized soil profiles (McVean, 1958).

(5) The taxa *Goodyera repens* and *Listera cordata* are represented within the field layer of the Scots pine woodland on various islands in the Morar archipelago. The taxon *Gooderya repens* is exclusive to the *Pinetum Hylocomieto-Vaccinetum* association *sensu* McVean and Ratcliffe (1962). Both taxa are characteristic elements in remanent native Scots pine woodland in Scotland. Furthermore, *Goodyera repens* is considered to be a potential indicator of ecological continuity of pine tree cover, by virtue of its biological association with the root system of *Pinus sylvestris* trees.

(6) The existence of dense thickets of young Scots pine trees surrounding parent trees is indicative that natural regeneration of *Pinus sylvestris* is proceeding on the Morar archipelago.

The evidence presented above clearly suggests that indigenous Scots pine woodland survives on the island archipelago at the western end of Loch Morar. Indeed, this community exhibits a range of floristic and physiognomic features which are common to native Scots pine woodland occurring elsewhere in Scotland. The existence of native Scots pine on the Morar archipelago is particularly significant. Indeed, the general absence of relict Scots pine from most of the extreme western and southwestern areas of Scotland (McVean and Ratcliffe, 1962), in conjunction with the restricted development of *Calluna* heath in these areas (McVean and Ratcliffe, 1962) suggest that there was probably a gradual restriction of the indigenous pine forest zone *sensu* McVean and Ratcliffe (1962), even upon acidic rocks in this region of Scotland (Birks, H.J.B., 1977). A swift transition from oak woodland to birch woodland is still evident on hill-slopes adjacent to many sea lochs in western Scotland; an intermediate woodland comprising Scots pine is not represented on these hill-slopes, in contrast with eastern regions of Scotland.

The Scots pine woodland community on the Morar archipelago represents a significant floristic variation in the woodland cover of the Morar Basin, which consists predominantly of mixed oak and birch woodland communities, corresponding with the zone of predominant oak forest with birch *sensu* McVean and Ratcliffe (1962) in western and southwestern Scotland. The existence of native Scots pine woodland on the archipelago, situated at latitude 56°58'N by longitude 5°47'W, indicates that the current geographical distribution of *Pinus sylvestris* var. *scotica* extends farther westwards on the Scottish mainland than the previously recorded western limit of 5°38'W, at Shieldaig, Ross-shire, Highland Region (Steven and Carlisle, 1959).

The epiphytic lichen flora within woodland communities can often indicate aspects of environmental change which have affected the tree layer during the past. In the following chapter, evidence is presented which suggests that the native Scots pine woodland community on the Morar archipelago, along with broad-leaved deciduous woodland communities on the hills surrounding Loch Morar exhibit sustained ecological continuity of high tree cover.

CHAPTER 4

EPIPHYTIC LICHEN COMMUNITIES

A forest community embraces a remarkable diversity of living organisms and micro-habitats. Indeed, the living trunk and branches of large forest trees provide a potential niche for a distinct and specialized community of epiphytic plants.

These arboreal epiphytes generally comprise species of Lichenes (lichens), Hepaticopsida (liverworts), Bryopsida (mosses) and Filicophyta (ferns), usually ranked in the preceeding order of significance.

The Lichenes (lichens) may be regarded as stable, consistent and identifiable biological associations between an individual algae and a fungus.

The shape of the thallus or body of a lichen is usually determined by the fungal partner. In some cases, however, where two or more types of algae are present in a lichen, usually a blue-green alga (Cyanophyceae) and a green alga (Chlorophyceae), they may produce very different forms within the single thallus.

The fungal partner within a lichen retains a heterotrophic physiology, which is characteristic of the fungi as a group, degrading dead or living organic substrates while the algal partner produces carbohydrates as a product of photosynthesis. The biological association apparently provides the fungal partner with a source of useful carbohydrates which are biochemically transferred within the lichen. The benefit to the algal partner is presently uncertain, however, the algae may acquire trace elements and solutes by virtue of the metabolic processes of the fungal partner.

Lichens can reproduce either asexually, by vegetative growth of fragments of the thallus, or sexually, by means of specialized spore-forming structures, termed soralia and isidia. The reproductive propagules are transported by many vectors, including wind, rain, insects and various other fauna, when a propogule comes to rest upon a suitable substrate, a complete lichen may eventually develop if the prevailing conditions are favourable for growth.

In the British Isles there are approximately 1,400 species of lichens; approximately 500 species occur frequently, while many others are very rare. The majority of these lichens comprise Ascomycetes fungi which produce spores within distinctive sac-like structures termed asci; a small minority of lichens contain either Basidiomycetes, Hyphomycetes or Phycomycetes fungal partners.

Lichens frequently comprise the dominant element of the bark-inhabiting communities of forested areas. In tropical regions their competitors include species of Filicophytes (ferns) and representatives of the families Bromeliaceae (Bromeliads) and Orchidaceae (Orchids).

In temperate regions their chief competitors are bryophytes; a range of bryophyte species can colonize the dead wood of trees which has fallen to the ground, while others can develop as true epiphytes on tree bark. In the British Isles, the bryophyte taxa *Hypnum cupressiforme* var. *filiforme* and *Dicranoweisia cirrata* and the liverwort *Frullania dilatata* are notable, examples which have been recorded growing in the tree canopy of the taxa *Quercus*, *Ulmus* and *Fraxinus excelsior*, in conditions of low relative humidity.

Under favourable conditions the cover which is created by the epiphytic flora may be so extensive that it entirely obliterates from view the superficial features of the underlying tree bark.

A number of factors determine the nature and species composition of the epiphytic lichen flora which develops upon a particular species of tree. The following factors, which are summarized under three main headings, are considered to be amongst the most important with respect to trees occurring in the British Isles:-

(1) BIOCHEMICAL FACTORS:

(a) The pH status (i.e. relative acidity) of the surface of the bark
(b) The base status of the bark
(c) The moisture retention and absorption properties of the bark
(d) The degree of leaching of the bark effected by rainwater
(e) The presence of tannins, resins and secondary products of metabolism in the bark
(f) The degree of impregnation of the bark by organic solutes
(g) The degree of exposure to air-borne pollution
(h) The degree of exposure to pollution arising from agricultural and industrial chemicals

(2) PHYSICAL FACTORS:

(a) The degree of exposure to incident light and illumination
(b) The directional aspect of the tree
(c) The relative humidity of the woodland environment

(3) PALAEOECOLOGICAL FACTORS:

(a) The ecological continuity of the tree cover
(b) The history and age of the woodland community

The biochemical and physical properties of bark are highly variable, even between different areas on a particular tree (Gilbert, 1970). Nevertheless, these factors are highly significant in their influence on the epiphytic communities. The pH status of tree bark is often of critical importance.

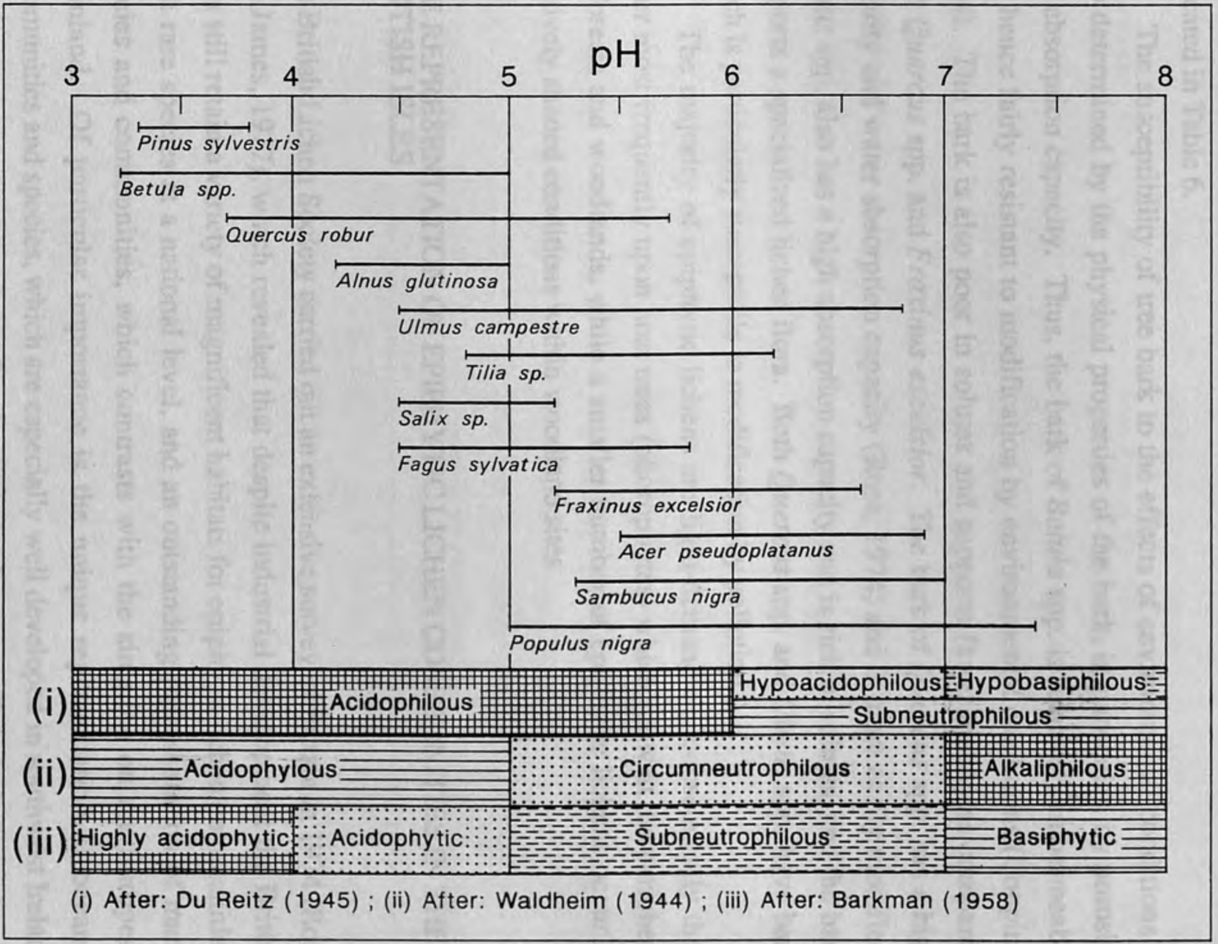
The pH status of the bark of a tree may be either acidic or alkaline, depending upon the particular species of the tree concerned. The following range of common tree species currently occurring in the British Isles, illustrates this case. Thus, *Quercus* species (oak), *Fraxinus excelsior* (ash), *Ulmus* species (elm), *Acer pseudoplatanus* (sycamore) and *Acer campestre* (field maple) have bark which is alkaline, while in contrast *Pinus sylvestris* var. *scotica* (Scots pine), *Betula* species (birch), *Alnus glutinosa* (alder) and *Fagus sylvatica* (beech) have bark wich is acidic (Barkman, 1958). The pH ranges of bark from common British trees are indicated in Figure 8.

The pH of tree bark is not constant, indeed, it may be altered by prevailing environmental conditions and ultimately by the epiphytic flora which develops on the tree bark. Thus, chemical enrichment resulting from the accumulation of wind-blown particles, sea salts and agricultural sprays, tend to increase the alkalinity of tree bark, e.g. Du Riez (1945) cited that dust impregnation caused the pH of a birch bark to increase from pH 4 to more than pH 6. The exudation of alkaline sap from wounds in the tree also alters the pH of the surrounding bark. In contrast, the leaching effect of rainwater results in a depletion of inorganic and organic solutes from tree bark and a reduction in the pH. The increase in acidity arises from the depletion of bases and the addition of dilute acids dissolved in rainwater. Sulphur dioxide released into the atmosphere, typically during combustion of fossil fuels, dissolves in rainwater to form sulphurous acid; subsequent oxidation results in the formation of sulphuric acid which constitutes the principal component of "acid rain".

The epiphytic flora can also influence and sometimes regulate the pH of the surrounding bark. The lichen thallus may trap allocthonous material and thereby passively affect the pH value. Active regulation of bark pH is also effected by some lichens which exude weak organic acids into the bark, and exchange Hydrogen ions for metal cations and vice versa, i.e. cation exchange takes place.

The physical form of the bark of a tree also appears to exert a subtle effect upon the development of an epiphytic lichen community, which is reflected in the relative abundance and diversity of individual species that develop upon a host tree. Thus, in the British Isles, trees belonging to the genus *Quercus* support at least 326 epiphytic lichens (Rose, 1974), a figure which accounts for 22 *per cent* of the recorded lichen species of the British Isles, and represents the greatest number supported by any British tree. *Fraxinus excelsior* (ash) supports at least

Fig.8 pH RANGES OF BARK FROM COMMON BRITISH TREES



(i) After: Du Reitz (1945) ; (ii) After: Waldheim (1944) ; (iii) After: Barkman (1958)

Source: Watson et al. (1988)

265 epiphytic lichens, which is ranked only second to *Quercus* spp. in the number of lichen taxa that it supports. Significantly, both *Quercus* spp. and *Fraxinus excelsior* exhibit tree bark which is alkaline in pH status and highly fissured in form. Undoubtedly, the fissured surface of the bark offers a range of potential niches for compatible lichen species. The number of lichen taxa recorded as epiphytes on selected trees in the British Isles (Harding and Rose, 1986) is indicated in Table 6.

The susceptibility of tree bark to the effects of environmental conditions is also determined by the physical properties of the bark, in particular, by porosity and absorption capacity. Thus, the bark of *Betula* spp. is relatively impermeable and hence fairly resistant to modification by environmental conditions (Coppins, 1984). The bark is also poor in solutes and supports fewer epiphytes compared with *Quercus* spp. and *Fraxinus excelsior*. The bark of *Quercus* spp. has a high porosity and water absorption capacity (Rose, 1974) and is more easily modified. *Ulmus* spp. also has a high absorption capacity and is rich in solutes, and the bark supports a specialized lichen flora. Both *Quercus* spp. and *Ulmus* spp. have bark which is particularly susceptible to modification by pollution.

The majority of epiphytic lichens are light-demanding, consequently they occur most frequently upon host trees (phorophytes) which grow at the periphery of forests and woodlands, while a smaller number of epiphytic lichens occur in relatively shaded conditions within woodland sites.

THE REPRESENTATION OF EPIPHYTIC LICHEN COMMUNITIES IN THE BRITISH ISLES

The British Lichen Society carried out an extensive survey of Britain in 1974 (Rose and James, 1977), which revealed that despite industrial development the British Isles still retain a variety of magnificent habitats for epiphytic lichen communities, with rare species at a national level, and an outstanding representation of many species and communities, which contrasts with the situation on the European mainland. Of particular importance is the unique representation of oceanic communities and species, which are especially well developed in southwest Ireland and the western coastal zone of Scotland. Indeed, western Britain is far richer in these communities than the oceanic regions of western Norway and western France, e.g. Brittany and Normandy. Although many of the oceanic species recorded in Europe are now known to occur widely in other parts of the world, especially the mountains of the Tropics, and in some sub-Tropical islands, e.g. Canaries and Azores, the actual associations are in many cases unique to Europe, and furthermore, within Europe they are best represented in the British Isles.

Table 6 - Numbers of lichen taxa recorded as epiphytes on selected trees in the British Isles

Tree	Number of lichen taxa	Ecological notes
Quercus (*Q. robur* and *Q. petraea*)	326	pH 3.8-5.7
Fraxinus excelsior	265	Bark fissured and rather similar to *Quercus*, but often of higher pH (5.4-6.6), lacks certain species of old *Quercus*
Fagus sylvatica	213	In spite of smooth bark, carries a flora very like *Quercus* in the New Forest, but has few epiphytes in chalk woodlands. Bark of low pH
Ulmus spp.	200	High water retention and pH (4.7-7.1), has a specialized flora
Acer pseudoplatanus	194	Carries a flora remarkably like *Ulmus* (pH high)
Salix (*S. cinerea* and *S. caprea)*	160	Quite rich especially in humid western areas
Corylus avellana	162	
Betula (*B. pubescens* and *B. pendula)*	134	Acid bark, pH 3.2-5.0
Acer campestre	101	Favourable bark of high pH, but of limited occurrence as a large tree
Alnus glutinosa	116	Acid bark (pH 3.5) of low water retentive capacity
Ilex aquifolium	96	Has a limited but specialized flora
Tilia spp.	83	Bark lacks water-retentive character, pH 4.1-4.7
Carpinus betulus	44	Limited by its smooth bark and its occurrence only in the driest part of England

Source: Watson *et al.* (1988), adapted from Harding and Rose (1986)

THE RICHNESS OF UNIQUE EPIPHYTIC LICHEN COMMUNITIES IN BRITAIN COMPARED WITH EUROPE

The paucity of epiphytic lichen communities in the oceanic regions of western Norway is due in part to the degree of latitude, since the northern limit of some southern oceanic species does not extend as far north as Norway. Perhaps more significantly, the ancient broad-leaved forests which are the main habitat for many oceanic species, have suffered far more modification than the remanent forests in western Scotland and some parts of northern England.

Some regions of western France, e.g. Brittany, are still very rich in oceanic species, however, most of the ancient forests have been extensively managed, with the elimination of most of the older trees and fallen timber. Furthermore, bryophyte-covered rock habitats, boulder-strewn forest floors and ravines, are poorly developed in this region compared with most of upland Britain.

The western Pyrenees mountains in southern France, and the north coast of Spain are reputed to be very rich in lichen species in some regions, however, detailed information is scarce, as these regions have not been studied extensively to date. Although these areas have incurred extensive forest modification, it is likely that the main factor which militates against the presence and abundancy of many species (in contrast to the situation in western Scotland and southwest Ireland) is the tendency toward hotter and drier summer conditions which prevail in southwestern France and northern Spain.

Factors which contribute to the lichenological importance of the British Isles include a complex and varied geology, and a climatic regime which permits the southerly extension of the geographical distribution range of many northern species, while also favouring the occurrence of southern species at latitudes exceptionally far north of their main geographical distribution range.

The British Lichen Society survey carried out in 1974 revealed that the mainland of Britain, and to a lesser degree the adjoining islands of the Inner Hebrides, are richer in relics of ancient primary broad-leaved woodland which have been relatively unmodified by man, than any other part of western or central Europe, north of the Pyrenees mountains. Although most of the individual sites are small, they collectively represent a considerable area of relatively unaltered ancient primary woodland.

The continuity of the forest environment, in terms of a humid micro-climate occasional gaps in the tree canopy (which permit light to penetrate to the ground layer) and the continuous presence of ancient trees, are considered to be responsible for the woodlands in Britain retaining a greater diversity of epiphytic and lignicolous lichens compared with western Europe. Furthermore, sites in Britain often exhibit an excellent representation of oceanic, southern oceanic and endemic elements, which is unrivalled elsewhere in western Europe, in terms of luxuriance and numbers of taxa per site.

On mainland Britain and the Inner Hebrides, there are currently 92 recorded broad-leaved sites with over 100 epiphytic lichen taxa per square kilometre. Of these sites 42 occur in England, 9 occur in Wales and 36 occur in Scotland. In addition, there are 7 sites of native Scots pine forest with over 100 lichen taxa per square kilometre. At Loch Creran in Argyllshire (Glasdrum National Nature Reserve) 208 epiphytic lichen taxa have been recorded from an ash *(Fraxinus excelsior)* woodland.

At several sites over 170 taxa have been recorded, while at nearly half of the sites over 150 taxa have been recorded. These figures conservatively indicate the diversity of lichen taxa present, and probably underestimate the diversity which exists at sites in Scotland.

Indeed, it is appropriate to illustrate the contrast in diversity of sites in Britain compared with western Europe. Data indicate that in France, north of the Pyrenees mountains, there are only 5 recorded sites with more than 100 epiphytic lichen taxa per square kilometre; one of these sites is the Forèt de Fontainbleau, whilst the remaining four sites all occur in Brittany. In Belgium, the Netherlands and Norway, no sites with 100 or more epiphytic taxa have been recorded, while in Denmark there are only 2 recorded sites with over 100 epiphytic taxa (Rose and James, 1977).

Recent studies have also revealed that magnificent relics of lichen associations associated with indigenous Scots pine also occur in the Highlands of Scotland. Although similar associations also occur in the Boreal coniferous forests of southern Norway, the sites in the western Highlands of Scotland also contain a unique assemblage of oceanic species, which are rare or absent in the Scandinavian forests. The finest surviving sites of Scots pine in Scotland include the forests of Guisachen, Strathfarrar and Coulin (Rose and James, 1977).

The epiphytic lichen communities which occur in the woodlands of upland Britain exhibit a remarkable diversity and state of development, which is unequalled in western Europe. Indeed, woodland sites which are farthest removed from sources of air-borne pollution often support a very diverse epiphytic lichen flora, particularly if the woodland contains old forest trees. Some lichen communities are especially well developed in western regions of Britain. Indeed, the western coastal zone of Scotland is particularly significant in this respect, and frequently exhibits an outstanding diversity of species and assemblages, which are often uniquely represented.

The communities which are particularly well developed in western regions of Britain include a number of species which have pronounced oceanic climatic affinities, along with other species which flourish abundantly in western regions, and yet exhibit less marked oceanic climatic affinities. These distinctive lichens include a range of large foliose types, e.g. *Lobaria amplissima, L. laetevirens, L. scrobiculata, Sticta fuliginosa, S. limbata* and *S. sylvatica,* and smaller species, e.g. *Pannaria rubiginosa, Parmelia laevigata, Parmeliella plumbea* and *Normandina pulchella.* Furthermore, some of the large species of the genera *Lobaria* and *Sticta* also grow upon a wider range of trees and age classes in western Scotland compared with less oceanic districts in Britain.

Epiphytic lichen floras which exhibit a high diversity of species are not wholly confined to western regions of Britain. Indeed, many important sites also occur in eastern and southern regions of Britain, where the annual rainfall is comparatively lower. Indeed, some epiphtyic lichen taxa appear to be intolerant of very high relative humidity, and exhibit a marked preference for eastern and southern regions, while remaining wholly absent from western regions of Britain.

Many extensive fragments of semi-natural, mixed broad-leaved deciduous woodland remain in Inverness-shire and in Ross and Cromarty. These woodland communities are significant in terms of their structure, floral diversity and primary character. Furthermore, they constitute the second major centre of geographical distribution of oceanic woodland lichens in Europe, being surpassed only in southwest Ireland. Indeed, within the British Isles many lichen taxa, e.g. representatives of the genus *Pseudocyphellaria*, appear to be largely or wholly confined to the western Highland coastal zone of Scotland (Rose, 1977a).

A number of epiphytic corticolous lichens, which exhibit a widespread geographical distribution in the upland woodlands of Britain, are frequently associated with large ancient trees which have spreading crowns. Some examples include the lichen taxa *Evernia prunastri, Hypogymnia physodes, Parmelia caperata, P. saxatilis, P. sulcata, Platismatia glauca, Ramalina farinacea*, and species of the genera *Alectoria, Physcia* and *Usnea*. Some of the richest areas for these lichens occur in woodland where the individual trees are spatially scattered and the tree canopy is relatively open. These lichen communities are particularly well developed in eastern districts of Britain and areas of relatively continental climate; many of the lichen species appear to be largely intolerant of deep shade and prefer instead situations where the tree canopy is relatively open.

Some lichen taxa appear to be currently restricted to old forest trees. This condition may reflect a low capacity of spore dispersion under prevailing climatic conditions, coupled with an inability of viable spores to become successfully established upon compatible host trees of younger age classes. These factors also affect the rarer epiphytic lichens and bryophytes, which therefore provide selective indicators of temporal continuity of tree canopy growth and high tree cover.

Old forest trees generally occur at sites which have remained relatively undisturbed or unmodified by anthropogenic activity for many centuries, by virtue of either geographical remoteness or historical accident. Thus, old forest trees frequently occur in the Royal Forests and deer parks, where the extant trees are often only a generation removed from the ancient forest which formerly occupied the site. Outstanding examples in Britain include the New Forest and Savernake Forest in Hampshire, and Cranborne Chase in Dorset, amongst others. Old forest trees also occur in the fragmentary woodland communities which occur predominantly in the upland areas of Britain, notably Exmoor and Dartmoor, western Wales, the Pennine Hills, the Cumbrian Lake District and many districts in the Highlands of Scotland.

THE RESTRICTION IN GEOGRAPHICAL DISTRIBUTION OF EPIPHYTIC LICHENS

Reliable evidence from literary sources and collections of lichen herbaria reveal a clear pattern of restriction, and even isolation, in the geographical distribution of many epiphytic lichen species in Britain. Indeed, a number of epiphytic lichens and bryophytes have declined in frequency during the last two centuries. Evidently, some lichen taxa produced viable spores and freely propagated new generations until the early to mid-nineteenth century, and thereafter became very rarely fertile or infertile in some regions, even within relatively unmodified woodland areas. Some taxa, however, continue to propagate freely in areas of high relative humidity, particularly in western Scotland (Hawksworth *et al.*, 1973, 1974).

A number of factors have undoubtedly contributed towards this phenomenon in Britain. The effect of pollution on lichens is now widely recognized as a primary factor (Ferry *et al.*, 1973). Indeed, recent investigations have demonstrated that a significant positive correlation exists between current lichen species diversity and abundance, with increasing distance from prevailing sources of pollution. The emergence of the Industrial Revolution in Britain during the late-eighteenth century, and the onset of production of significant quantities of air-borne pollution, is considered to be mainly responsible for the coincidental decline in lichen species from affected areas (Ratcliffe, 1977). Lichens are extremely sensitive to varying intensities and types of pollution, in particular Sulphur dioxide, which has been identified as a significant chemical pollutant. Indeed, this property has been exploited with respect to the use of lichens as indicators of air quality.

Rainwater in polluted areas frequently contains various concentrations of exotic chemicals and particulate material which cause an artificial enrichment of tree bark, and an accompanying change in the pH status of the bark. A subtle change in the biochemical status of the bark substratum is evidently sufficient to render the potential host tree unsuitable for colonization by selective lichen taxa. Consequently, a number of epiphytic lichen species are now absent from trees which occur within industrial and urban areas, and also from the most intensively cultivated rural regions. In contrast, various lichen taxa have remained fertile and continue to propagate freely, particularly in regions of oceanic climate in western Scotland, and significantly in areas which are remote from industrial pollution and urban development (Hawksworth *et al.*, 1974). Undoubtedly, the effect of anthropogenic activity on forest eco-systems has been significant in determining the floristic structure and composition of forest communities in Britain, dating from at least as the Neolithic Period, *circa* 5,000 years BP.

The outstanding diversity of epiphytic lichens which exists in the woodlands of upland Britain, particularly in the western Highlands of Scotland, is therefore remarkable. Indeed, their survival and success are due largely to favourable climatic conditions and remoteness from anthropogenic activity.

The composition and structure of indigenous epiphytic lichen communities is intrinsically dependent upon the dynamic processes which govern the development of forest eco-systems, in essence, the individual trees provide an ecological niche for colonization by epiphytic plants. Furthermore, the success and survival of this delicate biological relationship is dependent upon relative stability in environmental conditions, in particular, the ecological continuity of the canopy created by individual trees of the forest community. The process of colonization by epiphytes evidently occurs exceedingly slowly, at least under current conditions. Therefore, it is reasonable to suppose that temporal continuity in high tree cover is of paramount importance in determining the success and survival of epiphytic lichen communities. The history of woodland sites often reveals aspects of temporal change in floristic composition and structure of woodland vegetation. A change in the status of different tree species within the tree layer inevitably affects the floristic composition of the epiphytic flora. Thus, the floristic composition of the epiphytic lichen communities is partly determined by the legacy of environmental change which has ensued within the forest eco-system during the past.

In many regions of Britain, the indigenous primary forest evidently survived virtually intact and continuous in spatial extent until the Neolithic Period, *circa* 5,000 years BP. Under these conditions, the process of dispersal and colonization by epiphytic lichens and bryophytes was probably relatively uncomplicated, so that the epiphytic flora became ubiquitous in their appropriate ecological niches.

From the Neolithic Period onwards, however, a radical change ensued as the forest communities experienced drastic decimation and reduction in overall spatial extent. Most of the surviving forest communities experienced further modification and fragmentation by various forms of management and use during subsequent centuries; a process which has continued to the present. The remanent scattered forest communities which experienced least modification in Britain, now generally survive by virtue of either geographical remoteness or historical accident.

Despite the potential availability of suitable habitats for epiphytes within the fragmentary woodland communities, the process of re-establishment of an epiphytic flora has become increasingly difficult in sites of felled woodland which exhibit the regeneration of young trees, or in new plantations of trees. This situation has arisen mainly because the terrain surrounding woodland sites has also undergone modification and become unfavourable for lichen colonization. Hence, the physical communication between different communities of trees and epiphytes has become restricted; agricultural and forestry practice in Britain has been particularly significant in this process. Indeed, widespread land drainage and coppicing of woodland trees have resulted in a general desiccation of the landscape. Thus, even within relatively unaltered ancient woodland, some lichen species are currently very rarely fertile in lowland Britain, in contrast with the situation in the humid districts of western Scotland.

The significance of the broad-leaved deciduous woodland surrounding Loch Morar is indicated by the range and diversity of epiphytic lichens which flourish on the trees.

A representative example of oceanic broad-leaved deciduous woodland occurs at Kinsadel, which is situated approximately 500 metres from the western end of Loch Morar. This woodland surrounds Lochan a'Chleirich and extends around the nearby estuary of the River Morar. The woodland community comprises predominantly *Quercus petraea*, with *Corylus avellana* and *Betula pubescens* ssp. *odorata* in variable proportions. *Sorbus aucuparia* and *Ilex aquifolium* are frequent among the dominant trees. *Alnus glutinosa* is present on wet ground and waterlogged soils within the woodland, while *Salix*-carr is particularly well developed around the southern part of Lochan a'Chleirich. A view of this woodland looking southwards across Lochan a'Chleirich is illustrated in Plate 7.

The epiphytic lichen flora of the Kinsadel-Lochan a'Chleirich woodland was investigated by Dr Francis Rose during 1978, as part of a national survey and assessment of lichen habitats in Britain. This survey was organized by the British Lichen Society Woodland Working Party (Fletcher *et al.*, 1982). The field data collected by Rose (1978) and Day (1982) is reproduced in Table 7 with kind permission of Dr Rose. This survey revealed that the Kinsadel-Lochan a'Chleirich woodland contains a magnificent epiphytic lichen flora, including at least 112

Plate 7 Native deciduous woodland surrounding Lochan a' Chleirich, near Kinsadel, Morar

Table 7 - Census of epiphytic lichen taxa recorded from the Kinsadel-Lochan a'Chleirich woodland, Morar

Lichen Taxon	*Host Tree*
Arthonia didyma	-
Arthonia punctiformis	Quercus
Arthonia radiata	Corylus, Ilex, Quercus
Arthonia stellaris	Quercus
Arthonia tumidula	Corylus, Quercus
Arthopyrenia antecellans	Corylus
Arthopyrenia cinereopruinosa [+]	Corylus
Arthopyrenia lapponina	Corylus
Arthopyrenia punctiformis	Corylus, Ilex
Arthothelium ilicinum	Ilex
Baciolia biatorina	Quercus
Bryoria subcana	Quercus
Buellia disciformis	Quercus
Buellia erubescens	Quercus
Caloplaca ferruginea	Salix
Catillaria atropurpurea	Quercus
Catillaria pulverea	-
Cetrelia olivetorum	Betula, Salix, Sorbus
Chrysothrix candelaris	Betula
Cladonia chlorophaea	Quercus, Salix
Cladonia ciliata var. tenuis	-
Cladonia coniocraea	Betula, Salix
Cladonia macilenta	Betula
Cladonia polydactyla	Betula, Salix
Cladonia portentosa	-
Cladonia pyxidata	Salix
Cliostomumgriffithii	Ilex
Collema fasciculare	Salix
Collema subflaccidum	Corylus, Salix
Dimerella lutea	Quercus
Evernia prunastri	Betula, Salix
Fuscidea cyathoides var. corticola	Ilex
Fuscidea lightfootii	Ilex, Salix
Graphina anguina	-
Graphis elegans	Ilex
Graphis scripta	Corylus, Ilex
Haematomma caesium	Ilex, Salix
Haematomma elatinum	Betula, Salix, Sorbus
Hypogymnia physodes	Betula, Ilex, Quercus
Hypogymnia tubulosa	Betula, Salix
Lecanactis abietina	Betula, Ilex
Lecanactis homalotropa [1]	Corylus, Sorbus
Lecanora carpinea	-
Lecanora chlarotera	Corylus, Quercus, Salix
Lecanora expallens	Corylus, Ilex, Quercus
Lecanora jamesii	Salix
Lecanora symmicta	-
Lecidea carrollii	Salix
Lecidea cinnabarina	Betula
Lecidea granulosa	Betula
Lecidea uliginosa	-
Lecidella elaeochroma	Corylus, Ilex, Quercus, Salix
Lepraria incana	Quercus, Salix
Lepraria membranacea	-
Leptogium burgessii [1]	Corylus, Salix **
Leptogium cyanescens	-
Leptogium lichenoides	-
Leptorhaphis epidermidis	Betula

Lobaria amplissima	Quercus
Lobaria laetevirens	Corylus, Quercus, Salix
Lobaria pulmonaria	Betula, Corylus, Salix
Lobaria scrobiculata	Corylus, Quercus, Salix
Menegazzia terebrata	Betula, Quercus, Salix, Sorbus
Micarea peliocarpa	Betula
Micarea prasina	-
Micarea stipitata [1]	-
Mycoblastus sanguinarius	Betula, Quercus
Mycomicrothelia confusa	Corylus
Mycomicrothelia micula (auct.)	-
Nephroma laevigatum	Quercus, Salix
Nephroma parile	Corylus, Quercus
Normandina pulchella	Corylus, Quercus, Salix
Ochrolechia androgyna	Betula, Quercus
Omphalina luteovitellina	-
Opegrapha atra	Corylus
Opegrapha sorediifera	-
Opegrapha viridis	-
Opegrapha vulgata	Quercus
Pachyphiale cornea	Quercus
Pannaria (pityrea) conoplea	Corylus, Quercus, Salix
Pannaria rubiginosa	Corylus, Salix
Pannaria sampaiana	-
Parmelia caperata	Quercus
Parmelia crinita	Betula, Corylus, Quercus, Salix
Parmelia endochlora [1]	Betula
Parmelia glabratula	Betula, Corylus, Ilex, Quercus, Salix
Parmelia laevigata [1]	Betula
Parmelia perlata	Betula, Quercus, Salix
Parmelia revoluta	Salix
Parmelia saxatilis	Betula, Quercus, Salix
Parmelia sinuosa	Salix
Parmelia subaurifera	Corylus
Parmelia sulcata	Betula, Ilex, Salix
Parmelia taylorensis	Betula, Quercus
Parmeliella atlantica	Corylus, Quercus, Salix
Parmeliella jamesii	-
Parmeliella plumbea	Quercus, Salix, Sorbus
Parmeliella (corallinoides) tryptophylla	Corylus
Peltigera canina	Salix
Peltigera collina	Corylus, Salix
Peltigera horizontalis	-
Peltigera hymenina	Salix
Peltigera membranacea	Salix
Peltigera polydactyla	Salix
Pertusaria amara	Betula, Quercus
Pertusaria hymenea	Corylus, Ilex, Quercus
Pertusaria leioplaca	Corylus, Salix, Sorbus
Pertusaria multipuncta	Ilex, Salix, Sorbus
Pertusaria pertusa	Quercus
Pertusaria pupillaris	Betula
Phlyctis argena	Betula, Sorbus
Placynthiella icmalea	-
Platismatia glauca	Betula, Quercus, Salix
Porina leptalea	-
Pseudocyphellaria crocata [1]	Salix
Pseudocyphellaria intricata	Corylus, Salix
Pseudocyphellaria norvegica [1]	Corylus, Salix
Pyrenula laevigata	Quercus
Pyrenula macrospora	-
Pyrenula neglecta [1]	Corylus
Ramalina farinacea	Betula, Quercus, Salix
Sphaerophorus globosus	Betula, Quercus

Sphaerophorus melanocarpus	Betula, Quercus
Stenocybe septata	Ilex
Sticta canariensis [1]	Corylus
Sticta fuliginosa	Corylus, Salix
Sticta limbata	Corylus, Quercus, Salix
Sticta sylvatica	Corylus, Quercus, Salix
Thelotrema lepadinum	Corylus, Ilex, Quercus, Salix
Thelotrema monsporum 1	-
Thelotrema subtile [1]	Corylus
Tomasellia gelatinosa	
Usnea inflata	Quercus
Usnea subfloridana	Betula

+ - *Arthopyrenia cinereopruinosa* is described as *A. ranunculospora* Coppins and James (1988) *in* Coppins (1988)

[1] - species with a predominantly western distribution in Britain, confined to areas of high rainfall, with 180 or more wet days per year, i.e. 24 hour periods during which at least 1 millimetre of rainfall is recorded

* - taxa recorded by Day (1982)

Source: Rose (1978) and Day (1982)

species. The lichen flora also includes a range of taxa which currently exhibit a southern-oceanic geographical distribution; many of these taxa decline markedly within the deciduous woodlands which are situated northward of the Morar Basin. The Kinsadel-Lochan a'Chleirich woodland is described as one of the best woodland sites in West Inverness-shire (Rose, 1978). The woodland is designated as a Grade 3 Supplementary Site (Fletcher *et al.*, 1982), i.e. a woodland exhibiting the best lichen communities or assemblages with rare species or other features, in a context greater than a County, and hence of national importance.

The botanical significance of the native Scots pine woodland occurring on the Morar archipelago, indicated in the previous chapter, is further supported by evidence from surveys of the epiphytic lichen flora of two islands in the archipelago (Rose, 1977b, 1977c). The field data collected by Rose (1977) are reproduced in this chapter with kind permission of Dr Rose. The lichen data from these islands are discussed later in this chapter.

The diversity of epiphytic lichen taxa which occur within woodland communities in Britain may be assessed in the field, by means of recording the presence of individual taxa on standard coded mapping cards and site data sheets issued by the British Lichen Society. Furthermore, similarities and differences between individual woodland lichen floras may be readily assessed by comparing these records. Indeed, a useful method for evaluating epiphytic lichen communities in Britain was developed by James, Hawksworth and Rose (1977). The general principles of this method and ecological considerations are described below.

Field data pertaining to the British Lichen Society surveys of woodland sites within the catchment area of the Morar Basin, carried out by Rose (1977b, 1977c, 1978) and Day (1982) have been collated and analysed by the author in terms of the phytosociology of the lichen communities *sensu* James, Hawksworth and Rose (1977). In addition, the author also suggested that selective lichenological indicators recorded by the surveys, strongly indicate ecological continuity of high tree cover *sensu* Rose (1976) particularly at the Kinsadel-Lochan a'Chleirich woodland. Epiphytic lichen taxa recorded in the Kinsadel-Lochan a'Chleirich woodland have been designated in the text with an asterisk (*). The nomenclature of the lichen taxa have been checked by the author according to the British check-list (Hawksworth, James and Coppins, 1980), and up-dated in the case of *Arthopyrenia cinereopruinosa*, according to Coppins (1988).

THE PHYTOSOCIOLOGY OF EPIPHYTIC LICHEN COMMUNITIES IN BRITAIN

The phytosociology of epiphytic lichen communities in the British Isles was originally investigated and described by James, Hawksworth and Rose (1977).

In accordance with the conventions of the European and British Schools of Phytosociology, all plant communities which occur upon a particular substrate, e.g. bark, belong to one *class*, which may be sub-divided into *orders*. Where a particular substrate has a wide range of variation, e.g. bark occurring upon a living tree trunk, as distinct from dead branches and wood, etc., the *order* may be sub-divided into *alliances* (or federations). An alliance is denoted by the suffix *-ion,* which is applied to a given lichen genus or species name. Each alliance may contain one or more *associations* (or unions) which are denoted by the suffix -*etum.*

A detailed investigation of the epiphytic lichen communities in the British Isles (James *et al.*, 1977) revealed the existence of the following eleven distinct alliances upon tree bark; each alliance contains up to approximately twelve associations. The alliances are listed below in alphabetical order:-

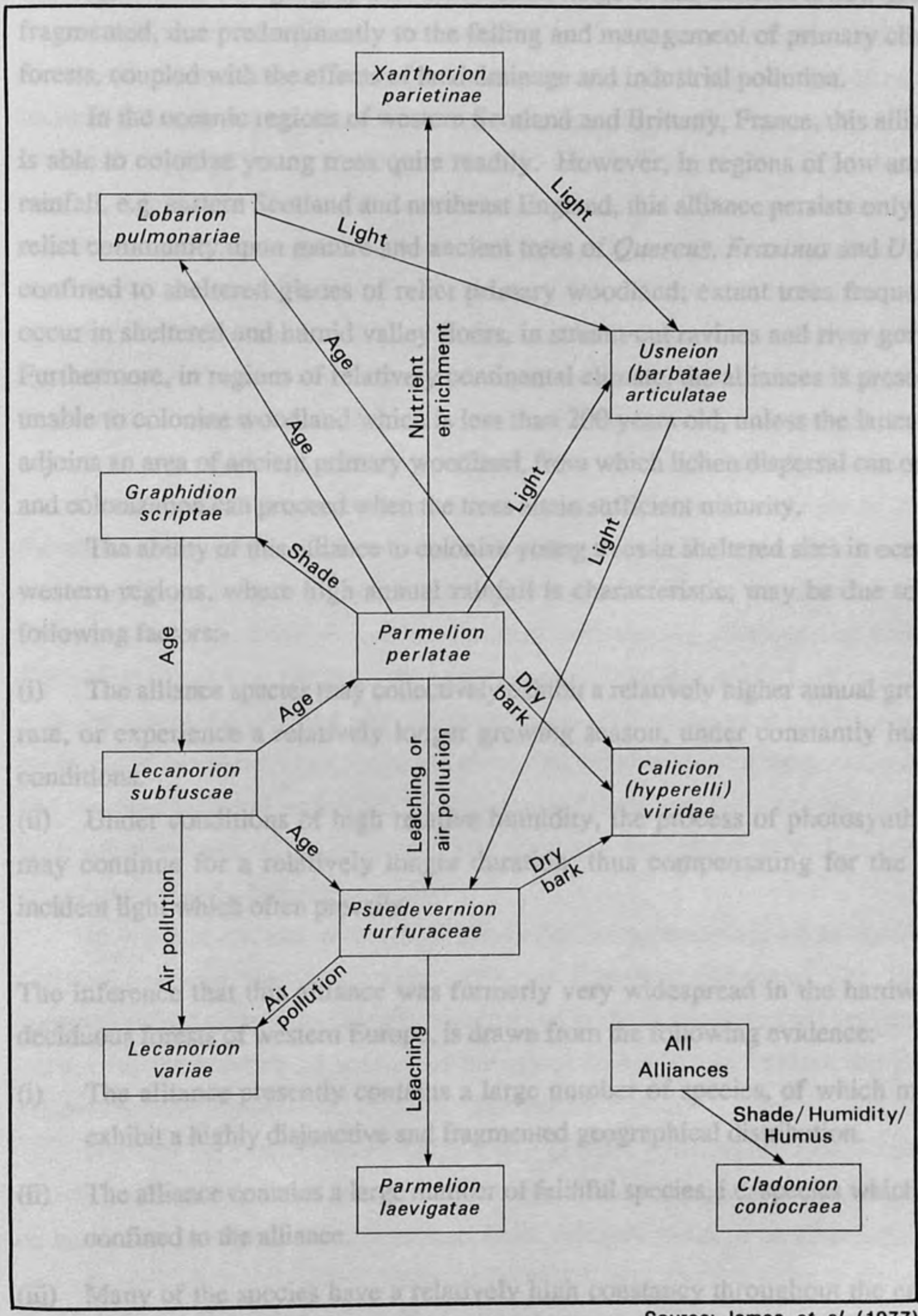
1. *Calicion (hyperelli) virideae*
2. *Cladonion coniocraeae*
3. *Graphidion scriptae*
4. *Lecanorion subfuscae*
5. *Lecanorion variae*
6. *Lobarion pulmonariae*
7. *Parmelion laevigatae*
8. *Parmelion perlatae*
9. *Pseudevernion furfuraceae*
10. *Usneion (barbatae) articulatae*
11. *Xanthorion parietinae*

The principal relationships between the epiphytic lichen alliances in the British Isles are illustrated in Figure 9. To date, seven alliances of epiphytic lichens have been recognized occurring predominantly in the woodlands of upland regions in Britain. These alliances are listed below in order of relative importance. The first three alliances are particularly significant in upland woodland:

1. *Lobarion pulmonariae*
2. *Parmelion laevigatae*
3. *Graphidion scriptae*
4. *Lecanorion subfuscae*
5. *Usneion (barbatae) articulatae*
6. *Cladonion coniocraeae*
7. *Pseudevernion furfuraceae*

The first five alliances are particularly well represented in the oceanic broad-leaved deciduous woodland communities surrounding Loch Morar. The distinguishing species and ecological characteristics of these alliances are described below.

Fig. 9 THE PRINCIPAL RELATIONSHIPS BETWEEN THE EPIPHYTIC LICHEN ALLIANCES PRESENT IN THE BRITISH ISLES



Source: James *et al.* (1977)

(1) THE *LOBARION PULMONARIAE* ALLIANCE

The *Lobarion pulmonariae* alliance is composed mainly of large foliose lichens and bryophytes, and appears to be the natural forest climax community in western Europe, occurring upon mature hardwood trees which have bark with a pH value in the range 5 to 6. The geographical distribution range of this alliance is now greatly fragmented, due predominantly to the felling and management of primary climax forests, coupled with the effects of land drainage and industrial pollution.

In the oceanic regions of western Scotland and Brittany, France, this alliance is able to colonize young trees quite readily. However, in regions of low annual rainfall, e.g. eastern Scotland and northeast England, this alliance persists only as a relict community upon mature and ancient trees of *Quercus, Fraxinus* and *Ulmus* confined to sheltered glades of relict primary woodland; extant trees frequently occur in sheltered and humid valley floors, in stream-cut ravines and river gorges. Furthermore, in regions of relatively continental climate, the alliances is presently unable to colonize woodland which is less than 200 years old, unless the latter site adjoins an area of ancient primary woodland, from which lichen dispersal can occur and colonization can proceed when the trees attain sufficient maturity.

The ability of this alliance to colonize young trees in sheltered sites in oceanic western regions, where high annual rainfall is characteristic, may be due to the following factors:-

(i) The alliance species may collectively exhibit a relatively higher annual growth rate, or experience a relatively longer growing season, under constantly humid conditions.

(ii) Under conditions of high relative humidity, the process of photosynthesis may continue for a relatively longer duration, thus compensating for the low incident light which often prevails.

The inference that this alliance was formerly very widespread in the hardwood deciduous forests of western Europe, is drawn from the following evidence:-

(i) The alliance presently contains a large number of species, of which many exhibit a highly disjunctive and fragmented geographical distribution.

(ii) The alliance contains a large number of faithful species, i.e. species which are confined to the alliance.

(iii) Many of the species have a relatively high constancy throughout the entire geographical range of the alliance. This is significant because the climate of the geographical range is not entirely oceanic.

(iv) The species of the alliance occur upon a wide range of deciduous woodland trees, being infrequent only upon *Alnus glutinosa*, which has bark with a low pH value.

The *Lobarion* alliance exhibit a relatively low diversity of species in eastern districts of Britain, often with only *Lobaria pulmonaria* and occasionally *L. scrobiculata* as representatives of the genus, while species of the genus *Sticta* are absent. In western districts of Britain, species diversity increases with the addition of species including *Lopazium pezizoideum, Parmeliella atlantica**, *Pseudocyphellaria crocata**, *P. intricata**, *Sticta canariensis** and *S. fuliginosa**. A particularly species-rich facies of this alliance occurs in sheltered valley-bottom woods in western Scotland, upon inclined boughs of old *Corylus avellana* and *Salix cinerea* ssp. *oleifolia* in wet carr woodland communities. This facies includes all four British *Lobaria* species (i.e. *L. amplissima**, *L. laetevirens**, *L. pulmonaria** and *L. scrobiculata**) which are fertile in this region, together with species of the genera *Pannaria**, *Parmeliella* and *Pseudocyphellaria*. Under constantly wet conditions *Cetrelia olivetorum**, *Menegozzia terebrata**, *Parmelia endochlora**, *P. laevigata** and *P. taylorensis** may also occur (these species are usually only found in the *Parmelion laevigatae* alliance) together with species of the genus *Leptogium*, particularly *L. burgessii** and the bryophyte genus *Ulota*. Significantly, this nodum is very distinctive when it is well developed, sharing affinities with both the *Parmelion laevigatae* alliance (although it occurs upon less acidic bark compared with the latter alliance), and with the *Graphidion scriptae* alliance by virtue of the presence of *Lecanora jamesii* communities. At suitable sites in western Scotland and southwest Ireland, under constantly wet conditions, tree branches with smooth bark often support *Graphina* spp. and *Graphis* spp. along with *Lecanactis homalotropa** and *Thelotrema subtile**.

In western Ireland, a facies of the *Lobarion* alliance occurs in the relict *Corylus avellana* woodlands which grow on limestone plateaux. This lichen community is similar in its floristic composition to the facies described previously, except for the absence of species of the genus *Lobaria*. In Ireland, the genus *Lobaria* is currently restricted to mixed-*Quercus* woodland.

Another distinctive lichen community of the *Lobarion* alliance occurs in *Fraxinus-Ulmus* woodland, particularly at sites where the woodland has developed on basic soils overlying either limestone, basic volcanic rocks, or on alluvium.

In addition to the species which are faithful to the *Lobarion* alliance, there is a particularly marked development of several other taxa, principally including species of the genera *Pannaria* (including *P. sampaiana**), *Parmeliella, Collema* (including *C. fasciculare**, *C. furfuraceum, C. nigrescens* and *C. subflaccidum**) and

Leptogium (including *L. azureum, L. burgessii*, L. cyanescens*, L. hibernicum* and *L. saturninum*). *Wadeana dendrographia* may also be present. This community is well developed in only a few regions of western Scotland, notably around Loch Sunart, Loch Morar, Loch Arkaig and on the Island of Mull, where it occurs in both open woodland and upon isolated or solitary trees. A few very rare British species also belong to this community and these include the eu-oceanic taxon *Arctomia delicatula*, along with *Collema occultatum* and *Pannaria ignobilis*. The latter taxon is a valley-bottom species occurring in the Central Highlands of Scotland, often upon trees which have *Bryoria capillaris* growing on their branches.

Some of the important component species of the *Lobarion pulmonariae* alliance represented in western Scotland are indicated in Table 8, taken from Rose (1988).

The *Lobarion pulmonariae* alliance is well developed in the oceanic broad-leaved deciduous woodland communities surrounding Loch Morar, where it exhibits a range of oceanic lichen taxa.

Lobaria pulmonaria is one of the largest British epiphytic lichens, often growing up to 18 centimetres in length. The upper surface of the lobed thallus is usually bright green in colour, however, during dry conditions it becomes brown in colour and papery in texture. The lower surface of the thallus is orange in colour, with brown filamentous hyphae. During reproductive phases, the upper surface of the thallus develops distinctive red coloured spore-producing soredia.

An example of the lichen *Lobaria pulmonaria* is illustrated in Plate 8. In this view, *L. pulmonaria* is surrounded by *Parmelia perlata, Usnea* ref. *subfloridana* and *Pertusaria* ref. *multipuncta*. These epiphytic lichens were recorded by the author during dry conditions in spring, growing on the bark of *Betula pubescens* ssp. *odorata*, by the River Morar.

Lobaria pulmonaria is now generally associated with oak woodland communities in upland areas of western Britain. During the nineteenth century this taxon was also recorded in eastern England, e.g. in Suffolk. Currently, it still survives in some southern countries of England, where it is often associated with *Quercus* spp. and *Fraxinus excelsior* trees in ancient woodland sites (Morris, 1979).

Table 8 - Important species in the European *Lobarion pulmonariae* alliance represented in western Scotland

Lobaria pulmonaria (L.) Hoffm.	a	*
L. scrobiculata (Scop.) DC.	a	*
L. laetevirens (Lightf.) Zahlbr.	a	*
L. amplissima (Scop.) Forss.	a	*
Sticta limbata (Sm.) Ach.	a	*
S. sylvatica (Huds.) Ach.	a	*
S. fulginosa (Hoffm.) Ach.	a	
S. canariensis (Ach.) Bory ex Delise	a	
Pseudocyphellaria crocata (L.) Vainio	a	
P. intricata (Delise) Vainio	a	
P. norvegica (Gyelnik) P. James	a	
Nephroma laevigatum Ach.	a	*
Peltigera collina (Ach.) Schrader	a	*
P. horizontalis (Huds.) Baumg.	a	*
Parmelia crinita Ach.	a	*
Pannaria conoplea (Ach.) Bory	a	*
P. rubiginosa (Ach.) Bory	a	*
P. mediterranea C. Tav.	a	
P. sampaiana C. Tav.	a	
Parmeliella atlantica Degel.	a	*
P. plumbea (Lightf.) Vainio	a	*
P. triptophylla (Ach.) Müll. Arg.	a	
P. testacea P. Jørg.	a	
Leptogium cyanescens (Rabenh.) Körber	a	
L. burgessii (L.) Mont.	a	
L. saturninum (Dickson) Nyl.	b	
L. teretiusculum (Wallr.) Arnold	a	
Collema nigrescens (Huds.) DC.	a	
C. subflaccidum Degel.	a	
C. furfuraceum (Arnold) Du Rietz	a	
Catillaria sphaeroides (Dickson) Schuler	a	
Pachyphiale carneola (Ach.) Arnold	a	
Thelopsis rubella Nyl.	a	
Biatorina atropurprea (Schaerer) Massal.	a	
Rinodina isidioides (Borrer) H. Olivier	b	
Porina coralloidea P. James	b	
Menegazzia terebrata (Hoffm.) Massal.	a	
Cetrelia olivetorum (Nyl.) Culb. & C. Culb.	a	
Phyllospora rosei Coppins & P. James	a	
Megalospora tuberculosa (Fée) Sipman	a	
Lopadium disciforme (Flotow) Vezda & Poelt	a	
Heterodermia obscurata (Nyl.) Trevisan	a	

a - present; probably or certainly frequent
b - present; but now apparently very rare
* - recorded in the Kinsadel-Lochan a'Chleirich woodland (Rose, 1978; Day, 1982)

Source: Rose (1988)

Plate 8 Epiphytic lichens growing on a native birch tree, near the River Morar

(2) THE *PARMELION LAEVIGATAE* ALLIANCE

The *Parmelion laevigatae* alliance is currently confined to regions of oceanic climate in western Europe; it typically occurs in upland woodland sites of western Britain, southwest Ireland and western Brittany, which receive a high annual rate of rainfall, i.e. within the range of 127-229 centimetres *per annum.*

Although this alliance is largely restricted to open communities of *Betula* and *Quercus* trees, it also occurs occasionally upon *Alnus glutinosa* trees, in situations of exposure to heavy rain and consequent leaching of the upper horizons of the tree bark. The pH value of the bark which supports this community ranges between pH 3.75-4.60, in contrast with the higher pH of the bark which supports the *Lobarion pulmonariae* alliance, where the pH value is usually above 5.0, and occasionally exceeds 6.0.

The occurrence of the *Parmelion laevigatae* alliance at a particular site appears to be determined primarily by the degree of exposure to rain-bearing winds, and secondarily by altitutudinal range.

This alliance is particularly characteristic of the following areas in Britain:

(1) The exposed mixed oak-birch woodlands occurring at between 50 to 360m altitude in western Scotland, and extending as far north as Wester Ross in Ross and Cromarty. This alliance is well represented in the woodland communities surrounding Loch Morar.

(2) The mixed oak-birch woodland occurring in areas of high annual rainfall in the Cumbrian Lake District.

(3) The upland oakwoods occurring at between 200 and 450m altitude in western Wales.

(4) The high-level oakwoods occurring at between 220 to 230m altitude around the periphery of Bodmin Moor in Cornwall.

(5) The exposed upland oakwoods occurring at between 360 to 440m altitude on Dartmoor in Devon, e.g. Black Tor Copse.

(6) The upper parts of valley oakwoods on Exmoor in Devon, and the Quantock Hills in Somerset.

Oakwoods which occur below the altitudinal ranges indicated for the respective areas may support *Lobarion pulmonariae* alliance, if the woodlands survive in a relatively undisturbed condition. The degree of transition between these two alliances varies considerably in Britain. Thus, in western Scotland there is a gradual transition between these communities on woodland trees, whilst in southern England, notably on Dartmoor and Exmoor, the transition is abrupt.

Fragmentary forms of this alliance also occur in valley bottoms throughout western Britain, occurring particularly upon the acidic bark of *Alnus glutinosa.* The *Parmelion laevigatae* alliance is characterized by *Mycoblastus sanguinarius*, Ochrolechia androgyna*, O. tartarea, Parmelia laevigata** and *P. taylorensis**. Other species which are largely faithful to this alliance include *Bryoria smithii, Cetrelia olivetorum*, Menegazzia terebrata*, Parmelia endochlora**, and in Scotland, the taxon *Pertusaria opthalmiza*. In addition, species of the genera *Cladonia* and *Sphaerophorus* are frequently important components in this alliance.

Where the alliance is established upon suitable trees in upland woodlands, an interesting saxicolous community may often develop upon rocks and boulder scree on the ground, which frequently includes a range of calcifugous bryophytes.

(3) THE *GRAPHIDION SCRIPTAE* ALLIANCE

In Britain, the *Graphidion scriptae* alliance is entirely restricted to deciduous trees which have smooth bark; it occurs particularly upon the young age-class of trees. This alliance is generally intolerant of air-borne pollution, and hence it occurs in areas which have relatively clean and uncontaminated air.

Where the alliance forms part of the epiphytic flora of a woodland community, it may occur thus as two distinct elements:

(i) As a pioneer community upon suitable trees

(ii) As an established community upon mature trees which have smooth bark, or upon trees which are restricted to situations where deep shade prevails.

This alliance is characterized by a wide range of crustose lichen species. Macrolichens often occur within its associations, which may be pioneers of subsequent successional stages.

In regions of oceanic climate in western Britain and western France, particularly in sheltered situations with high relative humidity, this alliance is frequently enriched with species of oceanic bryophytes, and foliose lichens which characterize both the *Lobarion pulmonariae* and *Parmelion laevigatae* alliances, respectively. This condition occurs particularly upon the inclined boughs of *Corylus avellana* and *Salix* species.

In regions of relatively continental climate, species of this alliance may occur upon the trunks of mature *Quercus* trees, living on the flat surfaces between the furrows of the bark. In regions of high annual rainfall, however, species of this alliance occur only upon trees which retain a smooth bark throughout their lives, e.g. *Corylus avellana, Sorbus aucuparia, Salix* spp., *Ilex aquifolium* and *Fagus sylvatica.* This alliance also occurs occasionally as a species-poor facies upon medium-age classes of *Betula* trees in oceanic regions of Britain.

Some hyper-oceanic lichen taxa also occur in the *Graphidion scriptae* alliance, these include species of the genus *Arthothelium* (excluding *A. ruanum*), e.g. *A. lirellans, Graphina ruiziana, Lecanactis homalotropa*, Leptorhaphis ischnobella, Parmentaria chilensis, Pyrenula dermatodes, P. laevigata** and *Thelotrema monosporum*.* These lichens also tend to occur upon suitable trees in situations where the *Lobarion pulmonariae* alliance exhibits a range of species belonging to the family *Pannariaceae,* along with a paucity of species belonging to the genera *Lobaria, Pseudocyphellaria* and *Sticta.* This alliance is well represented in the Glasdrum woods, Argyllshire, and in the woodland communities surrounding Loch Morar.

To date, several distinct associations have been recognized within the *Graphidion scriptae* alliance. The following provisional associations have been recognized in the woodlands of upland Britain:

(i) THE *GRAPHIDION SCRIPTAE* ASSOCIATION

The *Graphidion scriptae* association includes oceanic communities which occur on trees with smooth bark, in moderately shaded conditions. This association is dominated by some of the larger lirelliform crustose lichens, e.g. *Graphina anguina, Graphis elegans*, G. scripta*, Phaeographis dendritica* and *P. lyellii.* The taxon *Arthonia spadicea* also occurs frequently in this association.

(ii) THE *PYRENULATUM NITIDAE* ASSOCIATION

The *Pyrenulatum nitidae* association is characterized by extensive mosaics formed either solely of *Enterographa crassa,* or in conjunction with *Pyrenula nitida* and *P. nitidella.* This association occurs upon a wide range of deciduous trees with smooth bark, in deeply shaded conditions. Several species of particular importance include *Arthonia spadicea, A. tumidula, Graphis scripta*, Opegraphia atra*, O. viridis*, O. vulgata*, Pertusaria leioplaca** and *Phaeographis dendritica*; some of these species often becomes locally important. Transitions between the *Pyrenulatum nitidae* and *Graphidion scriptae* associations occur frequently.

(iii) THE *PERTUSARIETUM AMARAE* FACIES

The *Pertusarietum amarae* community is distinguished by the presence of shade-tolerant species, predominantly of the genus *Pertusaria*, which occur upon relatively less smooth tree bark than the *Pyrenulatum nitidae* association. The most important component species comprise *Pertusaria hymenea** and *P. pertusa**. Other species of this genus may become locally important, e.g. *P. hemisphaerica and P. leioplaca**. In ancient woodland, an additional characteristic element in the community comprises *Haematomma elatinum**, *Lecidea cinnabarina** and *Thelotrema lepadinum**. The *Pertusarietum amarae* community frequently intergrades with the *Pyrenulatum nitidae* association.

(4) THE *LECANORION SUBFUSCAE* ALLIANCE

The *Lecanorion subfuscae* alliance forms a pioneer community upon suitable young age-classes of trees, particularly in situations of high incident light. A characteristic feature of this alliance is the presence of distinctive mosaics, which are composed of taxa belonging to the genus *Lecanora*.

Within woodland communities in Britain, this alliance is represented solely by the *Lecanoretum subfuscae* association.

(i) THE *LECANORETUM SUBFUSCAE* ASSOCIATION

The *Lecanoretum subfuscae* association is characterized by mosaics which are composed of *Lecanora* species. Indeed, the most important components of the association include *Lecanora chlarotera**, *L. pallida* and *Lecidella elaeochroma**. This association is also includes a wide range of other taxa, in particular, *Arthonia radiata**, *Buellia griseovirens*, *Graphis scripta**, *Lecanora carpinea**, *L. confusa*, *L. expallens**, *L. intumescens*, *L. symmicta**, *Opegraph atra**, *Parmelia exasperata*, *P. subaurifera**, *Pertusaria leioplaca** and *Rinodina sophodes*, along with bryophytes belonging to the genus *Ulota*; many of these taxa occur frequently within this association. In slightly shaded situations the taxa *Haematomma elatinum**, *Lecanora jamesii** and *Phlyctis argena** also enter the association, particularly in western districts of Britain. This association had a widespread distribution in Britain.

(5) THE *USNEION BARBATAE* ALLIANCE

The *Usneion barbatae* alliance is composed of communities which are dominated by species of the genus *Usnea.* This alliance occurs upon trees which have acidic bark. Suitable host trees are generally colonized in situations where high incident light prevails. The following associations occur frequently in woodland communities of upland Britain:

(i) THE *CLADONIETO-USNEETUM TUBERCULATAE* ASSOCIATION

The *Cladonieto-Usneetum tuberculatae* association occurs in moderately shaded situations, where it is dominated by *Cladonia coccifera, C. pyxidata** and *C. squamosa.* In many upland regions, several species of the genus *Usnea* also enter this association and these include *Usnea flammea, U. fragilescens, U. inflata** and *U. subfloridana**.

(ii) THE *USNEETUM ARTICULATA-FLORIDAE* ASSOCIATION

The *Usneetum articulata-floridae* association is floristically similar to the previous association. However, it occurs in situations of high incident light in the uppermost branches of suitable host trees. This association has a marked southwestern geographical distribution in Britain.

(iii) THE *RAMALINETUM FASTIGIATAE* ASSOCIATION

The *Ramalinetum fastigiatae* association is dominated by species of the genus *Ramalina*, in particular, *R. baltica, R. calicaris, R. duriaei, R. farinacea**, *R. fastigiata* and *R. fraxinea.* The taxon *Ramalina pollinaria* may also become an additional dominant species under rare circumstances. This association occurs in situations of high incident light and moderate exposure and exhibits a widespread geographical distribution in Britain.

(iv) THE *USNEETUM FILIPENDULAE* ASSOCIATION

The *Usneetum filipendulae* association is dominated by the taxon *Usnea filipendula.* Other important taxa include *Alectoria sarmentosa, Bryoria capillaris*, and occasionally *Usnea hirta.* This association is particularly characteristic within relict Scots pine woodland in Scotland.

(6) THE *CLADONION CONIOCRAEAE* ALLIANCE

The *Cladonion coniocraeae* alliance is dominated by the taxon *Cladonia coniocraea**. This alliance forms communities upon the bases of tree trunks and also on peaty soils. In Britain this alliance is represented by the following two associations:

(i) THE *CLADONIETUM CENOTEAE* ASSOCIATION

The *Cladonietum cenoteae* association comprises lichen communities which are abundant in species of the genus *Cladonia*. This association occurs characteristically upon acidic substrates, including very dry and acidic bases of tree trunks, dead tree stumps and also peaty soils, within native Scots pine woodland in Scotland. This association includes the taxa *Cladonia botrytes, C. carneola, C. cenotea, C. deformis* and *C. rei*. Other taxa of this genus, which have a widespread geographical distribution range, also occur within the association, and these include *Cladonia furcata, C. gracilis* and *C. scrabruiscula*. This association is particularly well developed in Scots pine woodland at Glen More and Rothiemurchus in the East Central Highlands of Scotland.

(ii) THE *CLADONIETUM CONIOCRAEAE* ASSOCIATION

The *Cladonietum coniocraeae* association is dominated by the taxon *Cladonia coniocraea**. Other components of this association include the taxa *Cladonia chlorophaea**, *C. digitata, C. fimbriata, C. macilenta**, *C. pyxidata** and *C. squamosa*. This association exhibits a wide ecological amplitude, occuring upon the bases of shaded tree trunks, and occasionally extending its vertical range on the trunks of trees which grow in ravines and river gorges. This association also occurs upon rotting wood and peaty soils.

(7) THE *PSEUDEVERNION FURFURACEA* ALLIANCE

The *Pseudevernion furfuraceae* alliance occurs characteristically upon trees which have moderately acidic bark, e.g. *Betula* spp. and *Pinus sylvestris*. Host trees are colonized in situations where high incident light prevails.

This alliance is widespread throughout large areas of central and eastern Scotland, northern England and central Wales.

Several lichen taxa which characterize this alliance include *Bryoria fuscescens, Cetraria chlorophylla, Hypogymnia physodes*, H. tubulosa*, Ochrolechia androgyna*, Parmelia saxatilis*, P. sulcata*, Parmeliopsis ambigua, Platismatia glauca** and *Pseudevernia furfuracea.*

Within woodland communities in upland regions of Britain, this alliance is represented solely by the *Pseudevernion furfuraceae* association.

(i) THE *PSEUDEVERNION FURFURACEAE* ASSOCIATION

The *Pseudevernion furfuraceae* association comprises all the taxa which occur in the alliance. Under conditions of significant air pollution, however, the range of lichen taxa may exhibit a reduction in species diversity. Consequently, this association may be limited to *Hypogymnia physodes**, *Platismatia glauca** and *Parmelia saxatilis**, while occasionally, the taxon *Pseudevernion furfuracea* may be the sole representative. This association is widespread across large areas of central and northern Britain, where it often occurs luxuriantly both upon suitable host trees and siliceous rocks. In northern regions and upland areas of southwest Britain, the taxon *Bryoria fuscescens* is also commonly represented.

THE REPRESENTATION OF EPIPHYTIC LICHEN ALLIANCES IN THE KINSADEL-LOCHAN A'CHLEIRICH WOODLAND, MORAR

Lichen data recorded from the Kinsadel-Lochan a'Chleirich woodland by Rose (1978) and Day (1982) reveals that this oceanic broad-leaved deciduous woodland exhibits at least five epiphytic alliances *sensu* James, Hawksworth and Rose (1977).

(i) The *Lobarion pulmonariae* alliance is outstandingly represented by all four species of the genus *Lobaria*, along with a range of oceanic lichen taxa which are widely distributed on the woodland trees.

(ii) The *Parmelion laevigatae* alliance, which is particularly characteristic of mixed oak-birch woodland in western Scotland, exhibits the taxa *Parmelia caperata, P. perlata* and *P. revoluta* which approach the northern limit of their geographical distribution in this region of Britain.

(iii) The *Graphidion scriptae* alliance is well developed on trees which have smooth bark, and includes the following important taxa: *Arthonia stellaris, Arthothelium ilicinum, Lecanactis homalotropa, Lecanora jamesii* and

Pyrenula laevigata. This alliance also exhibits the taxa *Haematomma elatinum, Lecidea cinnabarina* and *Thelotrema subtile*, which are considered to be characteristic elements in old forests (Rose, 1976). The significance of the latter group of lichens is considered later in this chapter.

(iv) The *Lecanorion subfuscae* and *Usneion (barbatae) articulatae* alliances are also represented in this woodland.

(v) The epiphytic lichen flora contains a range of oceanic taxa, which are particularly well represented in *Salix*-carr woodland near Lochan a'Chleirich. These oceanic taxa include *Buellia erubescens, Catillaria pulverea, Lecanactis homalotropa, Micarea stipitata, Pannaria sampaiana, Parmelia endochlora, P. laevigata, P. sinuosa, P. taylorensis, Parmeliella atlantica, P. jamesii, Pseudocyphellaria crocata, P. intricata, P. norvegica, Pyrenula laevigata* and *Thelotrema subtile*.

The assessment and evaluation of current lichen floras from individual woodland sites in Britain, in conjunction with available historical evidence, has revealed aspects of environmental change at many important sites in Britain (Hawksworth, 1987). Indeed, correlation of individual woodland lichen floras has revealed the existence of characteristic taxa within woodland sites which have experienced ecological continuity of high tree cover (Rose, 1976). Furthermore, the compilation of an index of ecological continuity (Rose, 1976), based upon selected lichen taxa, has provided a potential method of determining continuity of high tree cover at different sites in Britain. The principles and methodology employed by Rose (1976) and the application of this index to lichen data recorded from woodland communities in the catchment area of the Morar Basin are described below.

LICHEN SPECIES DENSITY PER UNIT AREA OF WOODLAND SITES

There is a wide range of variation in the current lichen floras of different British woodlands, particularly with respect to the following criteria: species density, i.e. the number of taxa per unit area; species abundance, both in terms of the frequency of occurrence and cover value on individual host trees, and the species composition of the flora. Significantly, woodland of known antiquity, e.g. the New Forest in Hampshire, evidently support relatively larger numbers of lichen taxa per unit area, usually in the range of 120 to 150 taxa per square kilometre, compared with woodland of recent origin, or woodland with a history of major disturbance of tree canopy continuity, which typically support less than 40 taxa per square kilometre·

The relationship between the density of lichen taxa per unit area and the age and historical continuity of the tree cover was investigated by Rose (1976), who surveyed 102 lowland woodland sites in various areas of Britain. The data from this survey are presented in Table 9, reproduced from Table 1 in Rose (1976). Historical documentation of varying reliability was available for some sites, indicating the nature of forestry practice and the degree of continuity of high tree cover, while in other cases the information was either difficult to obtain or non-existent.

The survey carried out by Rose (1976) included the following categories of woodland sites:

(a) Mature to old stands of high forest of oak with glades, either medieval deer parklands or former Royal Forests or Chases, in many cases definitely known to have contained woodland during the Medieval Period, *circa* AD400 to AD1400. Furthermore, the sites in this category have not been managed as coppice woodland within the last few centuries.

(b) Naturally regenerated mature forest on former grazing land; two Sussex woodland sites in this category currently exhibit a similar structure to the sites in category (a), i.e. an unmanaged irregular high forest type. These sites are known to be on old common land which has almost certainly supported some woodland cover during the past. Furthermore, during the last few centuries, these sites were largely open pasture land which subsequently reverted to woodland by natural regeneration.

(c) Mature hardwood plantations within the New Forest, Hampshire.

(d) Mature high forest of oak, etc., known to have been clear-felled and replanted within the last 200 years.

(e) Old coppice woodland with oak or ash standards.

(f) Old Royal Forest, relatively unaltered in structure, but presently affected by significant air pollution (mean winter value of above 50μg SO_2 m^{-3}). The Epping Forest in Essex is unique in having extensive documentation of its former lichen flora (Hawksworth *et al.*, 1973). Data from the early nineteenth century indicate that this forest supported a density of lichen species comparable to several sites included in category (a). The current figure reflects a typical reduction in lichen populations under conditions of pollution stress.

A comparison between the species density data (Rose, 1976) for the categories of different woodland sites proves to be highly significant (Table 9). The majority of sites in category (a), with the exception of sites in eastern and central England, and some sites in Scotland, support over 100 lichen species per square kilometre. Indeed, many of the sites support a considerably larger number. This contrasts with data from the categories (b), (c), (d) and (e), which represent woodland sites which have experienced varying degrees of anthropogenic impact and modification, increasing in relative intensity from category (b) through to (e).

The sites in categories (b) and (c) have experienced severe environmental modification and desiccation. Consequently, the density of lichen taxa is considerably reduced compared with sites in category (a). These woodlands sites typically support between 30 to 80 lichen species per square kilometre.

The sites in categories (d) and (e) generally support a very low density of lichen species, within the range 13 to 70 lichen species per square kilometre, apparently irrespective of their location in the British Isles.

These data apear to indicate a significant negative correlation between lichen species density and the degree of anthropogenic modification within a woodland, excluding the case of hypertrophicated bark on trees which have colonized heavily pastured sites. The evidence from this comprehensive sample of woodland sites, selected by Rose (1976) as representative of the least altered relics of ancient British forests, suggests that the density of the lichen flora supported by primary hardwood forests, was probably of the order of at least 120 to 150 species per square kilometre. Furthermore, in view of the various changes which are known to have occurred in all British woodlands (Hawksworth *et al.*, 1974), the original densities of lichens may have been even greater than this estimated figure.

Table 9 - Lichen species density per unit area of woodland sites in Britain

Site	Species density per km^2, or less	Index of Ecological Continuity (Rose, 1974)	Revised Index of Ecological Continuity (Rose, 1976)
Section (a) Sites containing old high forest of oak with glades; either medieval parklands or former Royal Forests or Chases: many (indicated by [a]) are definitely known to have contained woodland in medieval times			
(i) Southwest England			
1. Boconnoc Park, Cornwall [a]	(188) 184	100	100
2. Trebartha Park, Cornwall	153	75	100
3. The Dizzard, Cornwall	128	55	85
4. Brownsham Woods, Devon	98	70	100
5. Arlington Park, Devon	121	60	75
6. Walkham Valley, Devon	116	60	75
7. Holne Chase, Devon [a]	106	70	100
8. Becka Falls, Devon	78	65	95
9. Horner Combe, Somerset [a]	(150) 146	70	100
10. Mells Park, Somerset	(115) 101	50	55
11. Melbury Park, Dorset [a]	(173) 162	85	100
12. Lulworth Park, Dorset	(115) 105	45	50
13. Cranborne Chase, Dorset and Wiltshire [a]	(148) 133	60	85
14. Longleat Park, Wiltshire [a]	(142) 133	75	95
15. Great Ridge Wood, Wiltshire	98	45	55
16. Savernake Forest, Wiltshire [a]	112 (c. 6 km^2)	50	60
(ii) New Forest, Hampshire [a]	259 (c. 36 km^2)	100	100
17. Mark Ash Wood	160	95	100
18. Vinney Ridge	116	80	100
19. Busketts Wood	159	90	100
20. Shave Wood	121	90	100
21. Wood Crates	135	70	80
22. Rushpole Wood	123	80	90
23. Great Wood	113	85	100
24. Bramshaw Wood	122	95	100
25. Bignell Wood	117	95	100
26. Lucas Castle Wood	132	95	100
(iii) Southeast England			
27. Uppark, Sussex [a]	131	45	65
28. Parham Park, Sussex [a]	(162) 149	50	60
29. St Leonards Forest, Sussex [a]			
(i) 1974	107	55	65
(ii) pre-1805	143	95	100
30. Eridge Park, Sussex [a]			
(i) 1975	(186) 177	70	85
(ii) 1842	(200) 191	85	100
31. Ashburnham Park, Sussex [a]	(151) 145	60	70
(iv) East Anglia			
32. Staverton Park, Suffolk [a]	65	30	35
33. Sotterley Park, Suffolk [a]	(92) 83	15	20

Site	Species density per km^2, or less	Index of Ecological Continuity (Rose, 1974)	Revised Index of Ecological Continuity (Rose, 1976)
(v) Midland England			
34. Wychwood Forest, Oxfordshire [a]	86	30	35
35. Brampton Bryan Park, Herefordshire [a]	(104) 94	50	50
36. Downton Castle Park, Herefordshire	67	35	40
(vi) Wales			
37. Gwaun Valley, Dyfed	117	55	65
38. Coedmore Woods, Dyfed	(117) 111	55	65
39. Coed Crafnant, Gwynedd	101	60	100
40. Shallow Falls, Bettws-y-Coed, Gwynedd	74	60	85
41. Coed Hafod, Clwyd	112	50	65
42. Glan Conwy, Clwyd	62	50	70
43. Coed Felinrhyd, Gwynedd	71	50	75
44. Coedydd Aber, Gwynedd	90	55	70
(vii) Northern England			
45. Shipley Wood, Durham			
(i) 1974	108	50	55
(ii) 1805	114	60	80
46. Great Wood, Borrowdale, Cumbria	102	65	95
47. Low Stile Wood, Borrowdale, Cumbria [a]	100	65	100
48. Gowbarrow, Cumbria	82	45	70
49. Naddle Low Forest, Cumbria [a]	73	25	40
50. Witherslack Woods, Cumbria	56	40	55
(viii) Apparently natural oakwoods in western Scotland			
51. Casmasine Woods, Loch Sunart	177	70	100
52. Ellary Woods, Loch Caolisport	127	65	100
53. Taynish Woods	98	40	65
54. Avinagillan, Loch Tarbert	91	55	90
55. Coire Buidhe, Loch Sunart	87	40	60
56. Loch na Droma Buidhe	77	40	70
57. Dorlin, Loch Moidart	71	40	70
58. Meall à Bhroin, Loch Sunart	100	50	80
59. Rubha aird Druimnich, Loch Sunart	92	40	70
60. Glasdrum, Loch Creran	85	30	65
61. Ard Trilleachan, Loch Etive	45	25	50
62. Bonawe Woods, Loch Etive	87	55	90
63. Dalnasheen, Appin	67	45	75
64. Kinauchdrach, Jura	61	40	55
65. Doire Dhonn, Jura	73	30	65
66. Ardmore, Islay	60	30	55
67. Coill'a'Chorra Ghiortein, Islay	55	30	45
Section (b) Sites with naturally regenerated mature forest on former common grazing land			
68. Ebernoe Common, Sussex	70	35	40
69. The Mens, Sussex	75	25	40

Site	Species density per km², or less	Index of Ecological Continuity (Rose, 1974)	Revised Index of Ecological Continuity (Rose, 1976)
Section (c) Mature hardwood plantations within the New Forest, Hampshire			
70. Pitts Wood Enclosure	54	30	40
71. Brockishill Enclosure	80	35	50
72. Pond Head Enclosure	31	20	30
73. South Bentley Enclosure	48	30	40
Section (d) Mature high forests of oak, etc., known to have been clear-felled and replanted within the last 200 years			
74. Dalegarth Woods, Eskdale, Cumbria	68	15	20
75. Nagshead Enclosure, Forest of Dean, Gloucestershire	16	0	0
76. Manesty Park, Derwent Water, Cumbria	20	0	0
77. Banneriggs, Grasmere, Cumbria	15	0	0
78. Rob Ragg Wood, Elterwater, Cumbria	12	0	0
79. Skelwith Force Wood, Lancashire	18	0	0
80. Claife Woods, Windermere, Cumbria	13	0	0
81. Low Coppice Wood, Grizedale, Lancashire	16	0	0
82. Anna's Wood, Coniston Water, Cumbria	13	0	0
83. Holme Wood, Loweswater, Cumbria	36	0	0
84. St Michael Penkevil, Cornwall	54	10	20
85. Cranford Cross, North Devon	24	5	5
86. Five Lords Wood, Quantocks, Somerset	29	10	10
87. Holford Combe, Quantocks, Somerset	50	20	25
88. Pamber Forest, Silchester, Hampshire	29	0	0
Section (e) Old coppice woodlands with oak or ash standards			
89. East Dean Park Wood, Sussex [ab]	70	40	40
90. Combwell Wood, Goudhurst, [ab] Kent	63	25	25
91. Brenchley Wood, Kent	44	5	5
92. Ham Street Woods, Kent	45	5	5
93. Near Loxwood, Sussex	33	0	0
94. Napwood, Frant, Sussex	45	5	5
95. Maplehurst Wood, Westfield, Sussex	54	5	10
96. Marline Wood, Hastings, Sussex	54	15	15
97. Foxley Wood, Norfolk [a]	15	5	5
98. Hayley Wood, Cambridgeshire [a]	35	5	5
99. Hintlesham Great Wood, Suffolk [a]	10	0	0
100. Felsham Hall Wood, Suffolk [a]	13	0	0
101. Park Coppice, Coniston, Cumbria	16	0	5
Section (f) Old Royal Forest, little altered in structure but now much affected by air pollution			
102. Epping Forest, Essex			
(i) 1974	38	5	10
(ii) early 19th century	(130) 109	25	30

b - these sites in section (e) contain areas of old trees in open high forest, and site 89 is known to have been a medieval deer park

Source: Rose (1976, Table I)

THE CONCEPT OF "OLD FOREST INDICATOR" LICHEN SPECIES AND THE (REVISED) INDEX OF ECOLOGICAL CONTINUITY

INDICATOR AND RELICT LICHEN SPECIES

While numerical comparisons of lichen species density data are both valid and useful they do not, however, indicate the floristic character of woodland lichen communities; a very wide range of ecological groups may occur even within a small woodland area. Indeed, different lichen species may be present for very different reasons.

Evidence of the antiquity of a woodland and the degree of modification from a primary forest state, may be determined by the recognition of indicator species known to be particularly sensitive to changes in the forest environment as a function of time, and whose presence or absence may indicate continuity or disturbance of this environment.

An examination of several hundred lowland deciduous woodlands in Britain and France, carried out by Rose (1976) in areas of low air pollution, revealed the following significant points:

(1) Certain species of lichen epiphytes occur in all, or nearly all woodlands which contain standard hardwood trees, whether these comprise old high forest, coppice-with-standards, or areas of mature oak plantation.

Table 10, reproduced from Table II in Rose (1976), cites a number of examples of these lichen species, which in many cases also occur equally commonly on oak and ash trees in open parkland, pasture, or minor roads, although less commonly by heavily used roads where pollution stress is signficant.

(2) A number of other lichen species normally only occur in mature or old stands of oak or mixed-oak high forest; where it proved feasible to establish the history of these sites in detail, the evidence indicated that these woodlands were very old, probably primary in origin, and furthermore, with some continuity of a high tree canopy, as distinct from coppice, dating from the Medieval Period at least.

Table 11, reproduced from Table III in Rose (1976), cites a number of examples of these lichen species:

Table 10 - Some lichen epiphytes common and general on *Quercus* (and on *Fraxinus*) in both woodland and in more open situations in unpolluted areas of lowland Britain

Calicium viride
Cetraria chlorophylla
Chrysostomum (Catillaria) griffithii
Evernia prunastri
Graphis elegans
G. scripta
Hypocenomyce (Lecidea) scalaris
Hypogymnia physodes
Lecanora chlarotera
L. expallens
Lepraria incana
Ochrolechia andogyma
O. (yasudae) subviridis
Parmelia caperata [a]
P. glabratula subsp. *glabratula*
P. perlata
P. revoluta [a]
P. saxatilis
P. subrudecta [a]
P. sulcata
Pertusaria amara
P. hemisphaerica
P. hymenea
P. pertusa
Phlyctis argena
Platismatia glauca
Pyrrhospora (Lecidea) quernea
Ramalina farinacea
Schismatomma decolorans [a]
Usnea subfloridana

a - species becoming rarer or absent in northern and eastern Scotland

Source: Rose (1976, Table II)

Table 11 - Some lichen epiphytes that appear to be "faithful" to mature or old stands of oak or mixed high forest

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Arthonia didyma
A. stellaris
Arthopyrenia (cinereopruinosa) ranunculospora
Bombyliospora pachycarpa
Caloplaca herbidella
Catillaria atropurpurea
C. pulverea
C. sphaeroides
Chaenotheca brunneola
Dimerella lutea
Enterographa crassa
Haematomma elatinum
Lecanactis (Opegrapha) lyncea
Lecanactis premnea
Lecidea cinnabarina
Leptogium burgessii
L. teretiusculum
Lobaria amplissima
L. laetevirens
L. pulmonaria
L. scrobiculata
Lopadium pezizoideum
Nephroma laevigatum
N. parile
Ochrolechia inversa
Pachyphiale cornea
Pannaria (pityrea) conoplea
P. mediterranea
P. rubiginosa
P. sampaiana
Parmelia arnoldii
P. crinita
P. horrescens
P. reddenda
Parmeliella plumbea
P. (corallinoides) triptophylla
Peltigera collina
P. horizontalis
Pertusaria velata
Phyllopsora rosei
Porina coralloides
P. hibernica
P. leptalea
Pseudocyphellaria crocata
P. (thouarsii) intricata
Pyrenula nitida
P. nitidella
Rinodina isidioides
Schismatomma niveum
Stenocybe septata
Sticta limbata
S. sylvatica
Strangospora (Biatorella) ochrophora
Thelopsis rubella
Thelotreme lepadinum

Source: Rose (1976, Table III)

In the British Isles, examples of these woodland communities include the following categories:-

(i) The "Ancient and Ornamental woodlands" of the New Forest; the only old Royal hunting forest which has remained, in part, open and free from active silvicultural management for some hundreds of years (Tubbs, 1964; Rose and James, 1974). The New Forest is unique in character in western Europe, particularly regarding its ecological features, which seem to compare more closely to the primary forest of the Holocene climatic optimum (*circa* 6,500 years BP) than to any other area of forest of comparable size in western Europe, westward of Poland.

(ii) The fragmentary relics of other Royal forests, or chases owned by the nobility, which have endured the last several centuries and exhibit continuity of forest habitat, despite modification by forestry practice and management, e.g. Savernake Forest in Wiltshire, Exmoor Forest, Boconnoc Wood in Cornwall, Horner Combe in Somerset, Wychwood Forest in Oxfordshire, Cranborne Chase in Dorset and Wiltshire, and until the nineteenth century, St Leonard's Forest in Sussex.

(iii) The woodland areas in deer parks established during the Medieval Period.

(iv) The woodland in remote districts of western and northern Britain, typically occurring on escarpments and steep-sided gorges and ravines, where active forestry practice has been minimal in effect, due to the remoteness or difficulty of the terrain, e.g. the high level oakwoods of Black Tor Copse on Dartmoor, Dizzard Cliff Wood in Cornwall, Camasine oakwood and Glasdrum Wood in Argyllshire, which exhibit lichen associations which are poorly represented beyond the British Isles.

These woodland communities are not, however, represented within the parks which were created by landscape gardening during the eighteenth century or subsequent to this era.

Substantive evidence indicates that many medieval deer parks and chases were formed from relict areas of forest and scrub, etc., which contained at least some fragments of primary virgin forest (Brandon, 1963). In contrast, most coppice-with-standards woodland which could be regarded as primary, in view of their continuance of woodland cover, have undergone drastic and continuous environmental modification as a consequence of the coppicing practice.

The lichen species cited in Table 11 (from Table III in Rose, 1976) may be regarded as "faithful" to the types of woodland associated with categories (a) to (d) of the woodland sites defined earlier in this chapter. These species are not, however, wholly constant in occurrence; some species exhibit a degree of restriction in their geographical distribution range in Britain, apparently due to climatic conditions, whilst other species are widespread in geographical distribution and variable in their frequency of occurrence. These "faithful" lichen species may represent relics of the primary forest epiphyte flora, analogous to some examples represented amongst the Coleoptera and Hemiptera of the insect fauna. Significantly, the presence of a sufficient diversity of these taxa may be reasonably regarded as indicative of continuity of the ancient forest canopy at a particular woodland site. Indeed, these taxa may be considered thus:

(i) As current ecological indicators of a particular forest environment in the present era.

(ii) As historical indicators of minimal environmental change (within certain critical limits) over a long period of time.

(iii) As relict species, which survive in currently isolated habitats, being unable to colonize new habitats which are distantly located from these refugia.

The author's examination of the census of lichen epiphytes recorded from the Kinsadel-Lochan a'Chleirich woodland (Table 8) has revealed that this site supports at least 29 out of 55 lichen taxa cited by Rose (1976) as "faithful" to mature or old stands of oak or mixed-oak high forest. These taxa are cited in Table 12. This is a significant representation, particularly as this woodland occurs in an upland situation. The lichen flora of broad-leaved deciduous woodlands in upland areas of Britain are often distinctive from lowland woodland sites, partly as a consequence of relatively higher annual precipitation, which causes intensive leaching of solutes from host tree bark. Indeed, upland woodlands also support a some particularly distinctive "faithful" lichen taxa, including *Bryoria smithii, Menegazzia terebrata, Ochrolechia tartarea* and *Parmelia laevigata.* The Kinsadel-Lochan a'Chleirich woodland exhibits both *Menegazzia terebrata* and *Parmelia laevigata.*

Table 12 - Lichen epiphytes recorded from Kinsadel-Lochan a'Chleirich woodland that appear to be "faithful" to mature or old stands of oak

Arthonia didyma
Arthonia stellaris
Arthopyrenia cinereopruinosa
Catillaria atropurpurea
Catillaria pulverea
Dimerella lutea
Haematomma elatinum
Lecidea cinnabarina
Leptogium burgessii
Lobaria amplissima
Lobaria laetevirens
Lobaria pulmonaria
Lobaria scrobiculata
Nephroma laevigatum
Pachyphiale cornea
Pannaria (pityrea) conoplea
Pannaria rubiginosa
Pannaria sampaiana
Parmelia crinita
Parmeliella (corallinoides) triptophylla
Parmeliella plumbea
Peltigera collina
Peltigera horizontalis
Pseudocyphellaria crocata
Pseudocyphellaria (thouarsii) intricata
Stenocybe septata
Sticta limbata
Sticta sylvatica
Thelotrema lepadinum

Source: derived from data by Rose (1978) and Day (1982)

THE (LICHEN) INDEX OF ECOLOGICAL CONTINUITY

Table 13 cites 20 lichen taxa selected by Rose (1974) who formulated an Index of Ecological Continuity of British deciduous woodland sites. These taxa are also cited as examples of epiphytic lichens which appear to be "faithful" to mature or old stands of oak or mixed-oak high forest (Rose, 1976).

The index of ecological continuity was applied by Rose (1974) to a number of woodland sites. An index value was derived by calculating the proportion of the "faithful" lichen taxa, cited above, which were present in a given woodland site, with the value expressed as a percentage. Index values for 102 British deciduous woodland sites are cited in Table 9, taken from Rose (1976). The original index was limited, however, by the localized geographical distribution of some of the selected lichen taxa, and by their variable frequency of occurrence. Consequently, this index was revised by Rose (1976) and augmented with a further 10 lichen taxa. The resulting 30 taxa, cited in Table 14 below (from Table V in Rose, 1976) occur reasonably frequently in woodland sites known to be ancient in both England and Wales; some lichen taxa which are known to be significant in Scotland, e.g. *Pseudocyphellaria* spp. were, however, excluded from the Index, on account of their current rarity in England and Wales.

The Revised Index of Ecological Continuity was applied by Rose (1976) to 102 British deciduous woodland sites (cited in Table 9; Table I in Rose, 1976). An Index value was derived by calculating the proportion of the "faithful" lichen taxa (cited in Table 14; Table V in Rose, 1976), up to a maximum of 20 taxa out of a total list of 30 taxa. This calculation may be summarized using the following formula, with the Revised Index value expressed as a percentage:-

$$\text{Revised Index of Ecological Continuity (RIEC)} = n/20 \times 100$$

where n = the number of "faithful" lichen taxa represented (up to a maximum of 20) in the woodland site, from the 30 taxa cited in Table 14 (Table V in Rose, 1976).

Occurrences of more than 20 taxa at a particular site are ignored, thereby providing a large enough sample of taxa to be sufficiently representative of the range of indicator species across different regions of the British Isles.

The Revised Index of Ecological Continuity for the 102 woodland sites selected by Rose (1976) are cited in the extreme right hand column of Table 9 (Table I in Rose, 1976), presented earlier in this chapter. Significantly, these Index

Table 13 - Lichens used to calculate the Index of Ecological Continuity

Arthonia didyma[a]
Catillaria atropurpurea[a]
C. sphaeroides[a]
Dimerella lutea[a]
Enterographa crassa[b]
Haematomma elatinum
Lecanactis premnea[b]
Lecidea cinnabarina
Lobaria laetevirens[a], *or*
L. amplissima[a], *or*
L. scrobiculata[a]
Lobaria pulmonaria[a]
Ochrolechia inversa[a]
Lecanactis (Opegrapha) lyncea[b]
Pachyphiale cornea[a]
Pannaria (pityrea) conoplea[a]
Parmelia crinita[a]
P. reddenda[a]
Peltigera horizontalis[a]
Sticta limbata[a]
Thelopsis rubella[a]
Thelotrema lepadinum

a - no longer present in midland and eastern England as a result of both environmental modification and air pollution
b - very rare, or absent, in the northern half of Britain

Source: Rose (1976, Table IV)

Table 14 - Lichens used to calculate the Revised Index of Ecological Continuity

Arthonia didyma
Arthopyrenia cinereopruinosa
Catillaria atropurpurea
C. sphaeroides
Dimerella lutea
Enterographa crassa[a]
Haematomma elatinum[a]
Lecanactis (Opegrapha) lyncea[a]
Lecanactis premnea[a]
Lecidea cinnabarina[a]
Lobaria amplissima
L. laetevirens
L. pulmonaria
L. scrobiculata
Nephroma laevigatum
Pachyphiale cornea
Pannaria (pityrea) conoplea
Parmelia crinita
P. reddenda
Parmeliella (corallinoides) triptophylla
Peltigera collina
P. horizontalis
Porina leptalea
Pyrenula nitida[a]
Rindodina isidioides
Stenocybe septata[a]
Sticta limbata
S. sylvatica
Thelopsis rubella
Thelotrema lepadinum

a - still existing in eastern England

Source: Rose (1976, Table V)

data exhibit a similar trend to the lichen species density data. The data which relates to the different categories of woodland sites are summarized below:-

Category (a): i.e. sites containing old high forest of oak with glades, either medieval deer parklands or former Royal forests or Chases, in many cases definitely known to have contained woodland during the Medieval Period.

RIEC values of 67 sites: - 50 or over for 91% of all sites, i.e. 61 sites
70 or over for 64% of all sites, i.e. 43 sites
80 or over for 51% of all sites, i.e. 34 sites
100 for 31% of all sites, i.e. 21 sites

Category (b): i.e. sites with naturally regenerated mature forest on former common grazing land (Sites 68 and 69)

RIEC values of 2 sites = 40

Category (c): i.e. sites of mature hardwood plantations within the New Forest, Hampshire (including Site 70)

RIEC values of 4 sites = 30 to 50

Category (d): i.e. sites of mature high forest of oak, etc., known to have been clear-felled and replanted within the last 200 years

RIEC values of 15 sites = 0 to 25

Category (e): i.e. sites of old coppice woodland with oak or ash standards

RIEC values of 13 sites = 0 to 40

Category (f): i.e. Old Royal Forest, relatively unaltered in structure, but presently affected by significant air pollution (Epping Forest, Essex)

RIEC value = 10 in 1974, compared with 30 during the early 19th century.

The census of lichen epiphytes recorded from the Kinsadel-Lochan a'Chleirich woodland (Table 8) indicates that this site exhibits at least 20 taxa which can be used to calculate the Revised Index of Ecological Continuity. These lichen taxa are cited below in Table 15.

The Revised Index of Ecological Continuity of the Kinsadel-Lochan a'Chleirich woodland was calculated using the following standard formula:

RIEC = n/20 x 100

The RIEC value for the Kinsadel-Lochan a'Chleirich woodland, Morar = 100. This index value corresponds with typical values determined by Rose (1976) for woodland sites in category (a), i.e. containing old high forest of oak with glades, as opposed to coppice.

Table 15 - Lichen taxa used to calculate the Revised Index of Ecological continuity of the Kinsadel-Lochan a'Chleirich woodland, Morar

Arthopyrenia cinereopruinosa
Catillaria atropurpurea
Dimerella lutea
Haematomma elatinum
Lecidea cinnabarina
Lobaria amplissima
Lobaria laetevirens
Lobaria pulmonaria
Lobaria scrobiculata
Nephroma laevigatum
Pachyphiale cornea
Pannaria (pityrea) conoplea
Parmelia crinita
Parmeliella (corallinoides) triptophylla
Peltigera collina
Peltigera horizontalis
Stenocybe septata
Sticta limbata
Sticta sylvatica
Thelotrema lepadinum

Source: derived from data by Rose (1978) and Day (1982)

The majority of sites with a high Index value (i.e. 80 to 100) in category (a) are distributed in southern and southwestern England, from the New Forest to Cornwall, and elsewhere in Sussex, central Wales, the Cumbrian Lake District and along the west coast of Scotland. The widespread geographical distribution of these woodland sites in Britain suggests that climatic factors, in particular, high annual rainfall, are unlikely to be primarily responsible for controlling lichen species density, or the occurrence of "faithful" lichen species in woodland sites. Indeed, sites which exhibit the highest lichen species densities and Index values are by no means exclusive to western Scotland (Table 9; Table I in Rose, 1976).

The Kinsadel-Lochan a'Chleirich woodland near Morar, has a Revised Index value of 100. Significantly, Rose (1976) cites seventeen sites of apparently natural oakwood in western Scotland (Table I; category (a)); five sites have a high Index value (i.e. 80 to 100), with two sites (51 and 52) represented by the Camasine Woods, Loch Sunart, and the Ellary Woods, Loch Caolisport which have an Index value of 100 respectively.

While the Revised Index of Ecological Continuity (Rose, 1976) is based upon lichen species which are regarded as "faithful" to old hardwood forests in lowland Britain, in particular, the New Forest (which necessarily has a better documented history of long continuity of environment than the majority of British woodland sites) it nevertheless comprises taxa which, apart from two cases, also occur widely in western Scotland.

The two sites in category (b) have Index values which compare with the sites in categories (d) and (e). However, the lichen species density values for category (b) are higher, possibly indicating some degree of ecological continuity at these sites. Indeed, this view correlates with historical documentation available for one of the sites (69) which is represented by The Mens, Sussex, which reveals that continuity of forest cover has certainly prevailed in localized areas at this site.

The four sites in category (c) are represented by plantations of hardwood trees within the New Forest, Hampshire. One site (73) was planted after AD 1750, while the remainder (70, 71 and 72) date from after AD 1800. These sites form a special case, for ancient woodlands either currently adjoin them (sites 71 and 73), or formerly adjoined them until the early nineteenth century (sites 70 and 72). The process of recolonization of the plantations by "faithful" lichen taxa from the adjoining ancient woodland probably occurred reasonably freely at these sites, in contrast with the sites in category (d).

The sites in category (d) are represented by mature high forests of oak, etc., known to have been clear-felled and replanted within the last 200 years; these sites are relatively more isolated from relict forest areas, both currently and probably at the time of plantation compared with sites in category (c). The low Index values for many sites in the Cumbrian Lake District is remarkable, particularly in view of the prevailing climatic conditions which are generally favourable for lichen growth, particularly the *Lobarion pulmonariae* alliance. One site (74) represented by Dalegarth Wood, Cumbria, comprises a mature oak woodland which superficially resembles woodland sites in category (a). The Index value (i.e. 20) is low, furthermore, elements of the *Lobarion pulmonariae* alliance are absent. Significantly, historical estate records indicate that most of this site was clear-felled and replanted around AD 1770.

The sites in category (e) are represented by old coppice woodlands, which generally have low Index values (i.e. 0 to 40). Furthermore, most of these sites do not support a diverse lichen flora. Historical records indicate that some form of woodland cover has existed since the early Medieval Period, at several of these sites (89, 90, 92, 94, 98 and 100). The practice of coppicing, which results in periodic desiccation of the woodland micro-climate, is evidently unfavourable for the survival of a range of lichen species, notably those taxa which are regarded as "faithful" to old hardwood forests.

Two of the sites (89 and to a lesser extent 90) in category (e) are interesting special cases. Site 89 is represented by East Dean Park Wood, Sussex. Historical records indicate that this site was partially forested during the early Medieval Period, when it became established as a deer park. Both sites 89 and 90 contain areas of old trees in open high forest. Indeed, East Dean Park Wood contains a large number of *Quercus* and *Fraxinus excelsior* trees which support lichen taxa including *Lobaria pulmonaria* and *Sticta limbata*. Furthermore, although this site comprises predominantly a coppice-with-standards woodland, it shares a greater affinity in terms of its flora, structure and history, with sites in category (a).

The site in category (f) is represented by Epping Forest, Essex. This site is an example of Old Royal Forest, which has survived relatively unaltered in floristic structure. A comparison between the Index value derived from early nineteenth century records, and the Index value for 1974 clearly reveals the significant effect of air-borne pollution on the epiphytic lichen flora at this site. Indeed, most of the epiphytic lichen flora recorded during the early nineteenth century has now been eliminated (Hawksworth *et al.*, 1973).

In southern and southwestern England, there are a number of woodland sites in category (a), in addition to the New Forest, which have remarkably high densities of lichen species, along with high Index values. These sites (1, 9, 11 and 14) are represented by Boconnoc Park, Cornwall; Horner Combe, Somerset; Melbury Park, Dorset and Longleat Park, Wiltshire. Historical evidence indicates that all these sites contained forest (enclosed as deer park) at the time of the Domesday Survey, *circa* AD 1085 to 1086. They all currently retain extensive areas of very old *Quercus* or *Quercus* with *Fagus sylvatica* stands, of sufficient density to retain a humid micro-climate between the individual tree trunks, while also permitting adequate illumination within the stands of trees. One site (30) represented by Eridge Park, Sussex, is particularly outstanding. Historical evidence indicates that this site was enclosed as a deer park about 800 years ago, and probably incorporated relict forest at the time of enclosure.

In northern England, Wales and Scotland, the woodland sites in category (a) have, in many cases, lower densities of lichen species compared with similar sites in southern England. Furthermore, most of these sites have relatively lower Index values. This may be a consequence of two geographical factors: firstly, the absence of many crustose lichens, normally associated with dry tree bark, from regions of high annual rainfall; secondly, the absence of many lichens from northern Britain which exhibit a more southern-European geographical distribution. Furthermore, although a number of hyper-atlantic and oceanic lichen taxa are more prevalent at sites farther northward and westward in Britain, they are not sufficiently numerous to compensate for the respective deficiency of southern and continental European taxa. Furthermore, hyper-atlantic taxa are not represented in the compilation and calculation of the Revised Index of Ecological Continuity (Rose, 1976).

In view of these points, it is both significant and remarkable that the Kinsadel-Lochan a'Chleirich woodland, near Morar, attains the maximum Index value of 100.

The comprehensive survey of British deciduous woodland sites and their associated lichen floras executed by Rose (1976), has elegantly demonstrated that the degree of ecological continuity of high tree cover within a woodland site may be determined by examining the following two features of the epiphytic lichen flora within a woodland site:

(i) The density of lichen species per unit area of woodland
(ii) The proportion of "faithful", i.e. relict forest lichen species in the flora, which may be regarded as environmental indicators.

The indicator lichen taxa included by Rose (1976) in the compilation of the (Revised) Index of Ecological Continuity, exhibit a widespread geographical distribution (at least in England, southward of the Cumbrian Lake District and Yorkshire). Furthermore, they also exhibit a significant positive correlation in distribution with areas of old woodland.

The Sussex Weald exhibits a better representation of forest lichen floras in comparison with East Anglia and most of the Midlands. This may be attributable to the topographic relief of the Weald, the relatively high annual rainfall, and the survival of more general woodland cover. Indeed, low relative humidity currently prevailing within many old woodland sites, which has arisen from extensive drainage of the landscape, coupled with a thinned woodland canopy in relatively dry climatic conditions, has resulted in the loss of most of the epiphytic and humicolous forest lichens, which can be used at other sites to determine an Index value of ecological continuity (Rose, 1976).

In order to compensate for a possible bias in the use of indicator lichen taxa which occur widely in geographical distribution in lowland Britain, Rose (1976) suggested that the Index could instead be confined to the members of the *Lobarion pulmonariae* alliance, i.e. comprising species of the genera *Lobaria, Nephroma, Pannaria, Parmeliella, Sticta,* etc. (Barkman, 1958; Rose, 1988). These taxa evidently fulfil the criteria of "Old Forest" indicators, with the exception of a few situations in western Scotland, where they appear to be able to freely colonize plantations of hardwood trees. Unfortunately, this amendment would result in a bias against many woodland sites in southern lowland Britain attaining significant values in an Index of this kind, principally because the majority of woodlands in southern Britain have lost a proportion of the species which comprise the *Lobarian pulmonariae* alliance.

The Revised Index of Ecological Continuity (Rose, 1976) nevertheless, provides a useful method of calculating, approximately, the continuity of high tree cover at British deciduous woodland sites.

EPIPHYTIC LICHEN COMMUNITIES OF INDIGENOUS SCOTS PINE WOODLAND

A number of areas of indigenous Scots pine woodland in Scotland, which appear to resemble remanent primary climax forest, support a high diversity of epiphytic lichen species, including many taxa which are not represented elsewhere in the British Isles. Indeed, the current geographical distribution range of some of these distinctive lichens occurs predominantly within the indigenous coniferous forests of Norway and Sweden. The lichen flora comprises taxa which occur widely throughout the Boreal coniferous forest, i.e. upon trees of *Pinus sylvestris, Betula* spp. and *Sorbus aucuparia,* and includes *Alectoria* spp., *Cetraria pinastri* and *Platismatia norvegica,* while other taxa appear to be confined to the oceanic western regions of Scandinavia and Scotland, and these include *Arthonia leucopellaea, Cavernularia hultenii* and *Platismatia norvegica.* Within Scotland there appears to be a distinctive assemblage of epiphytic lichens which are strictly confined to remanent Scots pine woodland. Significantly, mature plantations of Scots pine in the Scottish Highlands evidently do not exhibit these lichen taxa, while sub-spontaneous communities of pine, and mature coniferous plantations in lowland Britain, only support a very limited epiphytic lichen flora. Within Scotland, there exists a reasonable probability that colonization by these lichens has occured within coniferous plantations which are situated within close proximity of remanent native Scots pine woodland.

The existence of a diverse epiphytic lichen flora within remanent Scots pine woodland, which includes a number of distinctive lichen taxa, therefore offers the possibility of compiling a Boreal Forest Index, comparable in form with the Index of Ecological Continuity formulated for broad-leaved deciduous woodland in Britain (Rose, 1976).

Table 16, which is reproduced below from Table VII in Rose (1976), cites a number of lichen taxa which may represent "faithful" lichen epiphytes associated with indigenous Scots pine woodland, i.e. growing upon *Pinus sylvestris*, *Betula* spp., and *Sorbus aucuparia* trees in Scotland.

A larger number of lichen taxa which are regarded as characteristic of indigenous Scots pine woodland in Scotland are cited in Table 17 (Rose, 1977d). This table includes taxa which appear to be restricted to native Scots pine, while excluding other lichen taxa which exhibit a wider ecological distribution.

Paradoxically, the majority of epiphytic lichens which occur within remanent native Scots pine woodland, comprise taxa which rarely or never occur on *Pinus sylvestris*. Indeed, the taxa *Arthonia leucopellaea, Cavernularia hultenii* and *Platismatia norvegica* occur more frequently upon *Betula* spp. than on *Pinus sylvestris*. Furthermore, the foliose lichens which comprise the *Lobarion pulmonariae* alliance, are generally confined to *Sorbus aucuparia;* this tree additionally exhibits a range of distinctive oceanic and sub-oceanic taxa in western districts of Britain. The *Lobarion pulmonariae* alliance also occurs on *Betula pubescens* s.spp. and on *Quercus* spp. in sheltered situations. The *Lobarion pulmonariae* alliance is, however, uncommon on *Pinus sylvestris*.

The remanent native Scots pine woodlands exhibit considerable regional variation in the floristic composition of the epiphytic lichen flora. Indeed, these remanent woodland communities may reflect an relict continuum of variation in floristic composition and structure, possibly related to the prevailing oceanicity or continentality of the regional climatic conditions (Rose, 1977d). In western Scotland, the native Scots pine woodlands often contain broad-leaved deciduous tree species including *Sorbus aucuparia* and *Ilex aquifolium*, along with *Corylus avellana*, which typically support lichen taxa which comprise the *Graphidion scriptae* alliance. In contrast, the lichen flora of the native Scots pine woodland of eastern Scotland generally exhibit a reduced diversity of species.

Table 16 - Possible "faithful" lichen epiphytes of Boreal coniferous forest in Scotland

Alectoria sarmentosa sub sp. *sarmentosa*
Arthonia leucopellaea
Bryoria (Alectoria) capillaris
Bryoria (Alectoria) lanestris
Buellia schaereri
Cavernularia hultenii
Chaenotheca spp.
Haematomma elatinum
Hypocenomyce (Lecidea) friesii
Lecidea cinnabarina
Lecidea ochrococca
Platismatia norvegica
Usnea (extensa) glabrescens

Source: Rose (1976, Table VII)

Table 17 - Lichen epiphytes that are characteristic of indigenous Scots pine woodland

Lichen taxon	Host tree
Alectoria sarmentosa	*Betula, Pinus*
Arthonia leucopellaea	*Betula, Ilex, Pinus, Sorbus*
Biatorella resinae	*Pinus*
Bryoria capillaris	*Pinus*
Bryoria furcellata	*Betula, Pinus*
Bryoria lanestris	*Pinus*
Buellia schaereri	*Pinus*
Calicium glaucellum	*Pinus*
Calicium parvum	*Pinus*
Catillaria spp.	-
Cavernularia hultenii	*Betula, Pinus, Sorbus*
Cetraria pinastri	*Pinus*
Cetraria sepincola	*Betula*
Chaenotheca brunneola	*Pinus*
Chaenotheca chrysocephala	*Pinus*
Chaenotheca hispidula	*Alnus*
Chaenotheca trichialis	*Alnus, Betula, Pinus*
Chaenotheca xyloxena	*Alnus*
Chaenotheciopsis epithallina	*Pinus*
Chaenotheciopsis lignicola	*Pinus* lignum
Chrysothrix chrysopthalma	*Pinus*
Coniocybe pallida	*Alnus*
Coniocybe peronella	*Alnus, Betula*
Coniocybe sulphurea	*Alnus, Betula*
Cyphelium inquinans [a]	*Pinus*
Cyphelium tigillare	*Pinus* lignum
Haematomma caesium	*Pinus, Sorbus*
Haematomma elatinum	*Pinus*
Hypocenomyce friesii	*Pinus*
Lecidea botyrosa	*Pinus*
Lecidea cinnabarina	*Betula, Pinus, Sorbus*
Lecidea fuscescens	*Pinus*
Lecidea hypopta	*Pinus*
Lecidea ochrococca	*Betula, Pinus, Sorbus*
Lecidea turgidula	*Pinus*
Microcalicium subpedicellatum	*Pinus*
Mycoblastus affinis	*Pinus, Pinus* lignum
Mycoblastus fucatus	*Pinus* lignum
Parmeliopsis aleurites [a]	*Pinus*
Parmeliopsis ambigua [a]	*Pinus*
Parmeliopsis hyperopta	*Pinus*
Platismatia norvegica	*Betula, Pinus*
Usnea filipendula	*Pinus*
Usnea hirta	*Pinus*
Xylographa trunciseda	*Pinus* lignum
Xylographa vitiligo	*Pinus* lignum

[a] Lichen taxa which are presently widespread in geographical distribution in Britain, occurring on wooden palings or in areas subjected to pollution, but probably originally associated with native Scots pine communities

Source: Rose (1977d)

Within the indigenous Scots pine woodlands there is, however, a distinctive assemblage of epiphytic lichen taxa which is confined to either the bark or lignum of *Pinus sylvestris*. This group comprises taxa belonging to the families *Caliciaceae* and *Cypheliaceae*, including the genera *Calicium, Chaenotheca, Chaenothecopsis, Coniocybe, Cyphelium* and *Microcalicium*, along with the taxa *Hypocenomyce friesii, Lecidea botyrosa, L. hypopta* and *L. ochrococca.*

The principal sites of oceanic western Scots pine communities are represented at Barisdale Forest in Knoydart, Black Mount Woods on Rannoch Moor, Tyndrum, Coille na Glas Leitire by Loch Maree, Coulin and Shieldaig in Wester Ross. The epiphytic lichen flora of these western Scots pine communities is characterized by a relative scarcity of taxa belonging to the genus *Alectoria*, and a scarcity of taxa belonging to the family *Caliciaceae*. In contrast, the *Lobarion pulmonariae* alliance is abundantly represented, along with oceanic taxa, on trees other than *Pinus sylvestris*. Indeed, *Thelotrema subtilis* is often present on *Corylus avellana* and *Sorbus aucuparia*. The taxon *Cavernularia hultenii* also occurs frequently in the epiphytic lichen flora.

The botanical significance of the Scots pine woodland on the Morar archipelago, discussed previously in Chapter 3, is further emphasized by the range and diversity of epiphytic lichens which flourish on the woodland trees of two islands in the Morar archipelago, which were investigated by Dr Francis Rose during 1977. Field data collected from an-t Eilean Meadhoin (Rose, 1977b) and Eilean a'Phidhir (1977c) are reproduced in Tables 18 and 19 with kind permission of Dr Rose.

The woodland community on Eilean a'Phidhir, the largest island within the Morar archipelago, was reported by Rose (1977c) to be comprised of *Pinus sylvestris* with *Sorbus aucuparia, Salix* and *Betula*. The taxon *Goodyera repens* was also present in the ground layer.

The woodland survey on an-t Eilean Meadhoin, the second largest island in the Morar archipelago, was reported by Rose (1977b) to be comprised of very old *Pinus sylvestris*, with *Sorbus aucuparia, Salix, Betula, Taxus baccata, Quercus* and *Populus tremula*. The presence of *Populus tremula* (aspen) on this island is notable because it occurs typically as an occasionally or rare tree species within indigenous Scots pine woodland (Steven and Carlisle, 1959). The presence of *Goodyera repens* in the ground layer vegetation among very old *Pinus sylvestris* trees on Eilean a'Phidhir is also significant. *Goodyera repens* develops a unique mycorrhizal relationship with the root system of *Pinus sylvestris*, usually at sites which exhibit continuity of Scots pine tree cover. Indeed, this taxon may represent a potentially reliable indicator of ecological continuity of high tree cover (Ratcliffe, 1977).

Table 18 - Census of epiphytic lichen taxa on an-t Eilean Meadhoin, Loch Morar

Lichen taxon	Host tree
Arthonia cf. stellaris	*Sorbus*
Arthopyrenia antecellans	*Sorbus*
Buellia schaereri	*Pinus*
Chrysothrix chrysopthalma	*Pinus*
Cladonia coniocraea	*Betula*
Cladonia squamosa	*Betula*
Evernia prunastri	*Betula*
Haematomma caesium	*Pinus*
Haematomma elatinum	*Betula, Pinus, Populus*
Hypogymnia physodes	*Betula, Pinus*
Hypogymnia tubulosa	*Pinus*
Lecanora chlarotera	*Quercus, Sorbus*
Lecanora expallens	*Populus*
Lecidella elaeochroma	*Sorbus*
Lepraria incana	*Pinus, Taxus*
Lobaria laetevirens	*Sorbus*
Lobaria pulmonaria	*Betula, Populus, Quercus, Sorbus, Taxus*
Lobaria scrobiculata	*Betula, Populus, Sorbus*
Menegazzia terebrata	*Betula*
Micarea stipitata [1]	*Populus*
Normandina pulchella	*Quercus, Salix*
Ochrolechia androgyna	*Betula, Populus*
Ochrolechia subviridis	*Betula, Taxus*
Parmelia crinita	*Betula, Pinus, Populus, Sorbus*
Parmelia glabratula	*Pinus*
Parmelia glabratula ssp. *fuliginosa*	*Betula, Quercus, Salix, Sorbus, Taxus*
Parmelia laevigata [1]	*Betula, Populus*
Parmelia perlata	*Betula, Populus, Taxus*
Parmelia revoluta	*Betula, Pinus*
Parmelia saxatilis	*Betula, Pinus, Sorbus, Taxus*
Parmelia sulcata	*Pinus*
Parmelia taylorensis	*Betula*
Parmeliella atlantica	*Sorbus*
Parmeliella plumbea	*Quercus, Salix, Sorbus*
Parmeliella triptophylla	*Quercus*
Parmeliopsis hyperopta	*Pinus*
Peltigera membranacea	*Betula, Populus*
Pertusaria hymenea	*Populus, Quercus, Sorbus*
Pertusaria opthalmiza	*Betula*
Pertusaria pertusa	*Betula*
Platismatia glauca	*Betula, Pinus, Populus*
Pyrenula laevigata	*Sorbus*
Sticta sylvatica	*Populus, Sorbus*
Usnea fragilescens	*Populus*
Usnea subfloridana	*Betula, Pinus*

[1] species with a predominantly western distribution in Britain, confined to areas of high railfall, with 180 or more wet days per year, i.e. 24 hour periods during which at least 1 millimetre of rainfall is recorded

Source: Rose (1977b)

Table 19 - Census of epiphytic lichen taxa on Eilean a'Phidhir, Loch Morar

Lichen taxon	Host tree
Buellia schaereri	*Pinus*
Cladonia chlorophaea	*Pinus, Sorbus*
Graphis elegans	*Betula*
Haematomma elatinum	*Pinus*
Hypogymnia physodes	
Lecanora chlarotera	*Sorbus*
Lecanora expallens	*Betula*
Lecidea elaeochroma	*Salix, Sorbus*
Lepraria incana	*Sorbus*
Lobaria laetevirens	*Sorbus*
Lobaria pulmonaria	*Sorbus*
Lobaria scrobiculata	*Sorbus*
Micarea cinerea	*Pinus*
Mycoblastus sanguinarius	*Pinus*
Nephroma laevigatum	*Salix, Sorbus*
Normandina pulchella	*Sorbus*
Pannaria rubiginosa	*Sorbus*
Parmelia glabratula	*Sorbus*
Parmelia perlata	*Pinus*
Parmelia saxatilis	*Pinus, Sorbus*
Parmelia sinuosa	*Pinus*
Parmelia sulcata	*Pinus*
Parmeliella plumbea	*Salix, Sorbus*
Parmeliopsis hyperopta	*Pinus*
Phlyctis argena	*Sorbus*
Usnea flammea	*Pinus*
Usnea subfloridana	*Pinus*

Source: Rose (1977c)

A comparison between the characteristic features of the epiphytic lichen flora of the oceanic western Scots pine woodland in Scotland and the Scots pine communities of the Morar archipelago, reveals a number of remarkable similarities. In particular, the presence of broad-leaved deciduous trees, which form an intrinsic floral element within the tree layer of western Scots pine woodland, exhibit a characteristic development of the *Lobarion pulmonariae* alliance, which contrasts with its absence from *Pinus sylvestris* trees. The taxa *Lobaria laetevirens, L. pulmonaria* and *L. scrobiculata* were recorded on *Sorbus aucuparia* trees from both islands, and also variously distributed upon *Betula pubescens, Populus tremula, Quercus* and *Taxus baccata*. This reflects the general pattern of development of the *Lobarion pulmonariae* alliance in the native Scots pine woodland of western Scotland.

The broad-leaved deciduous trees within the Scots pine woodland on the Morar archipelago additionally exhibit a range of oceanic lichen taxa, including *Parmelia atlantica* and *Pyrenula laevigata* on *Sorbus aucuparia*, along with *Micarea stipitata* and *Parmelia laevigata* on *Populus tremula*.

Lichen taxa associated with the *Graphidion scriptae* alliance are represented by *Arthonia* ref. *stellaris* and *Pyrenula laevigata* on the smooth bark of *Sorbus aucuparia*, along with *Graphis elegans* on *Betula pubescens*. The taxon *Haematomma elatinum* is also represented on a range of host trees including *Populus tremula, Betula pubescens* and *Pinus sylvestris*.

Lichen taxa associated with the *Lecanorion subfuscae* alliance are represented by *Lecanora chlarotera* on *Betula pubescens, Quercus* ref. *petraea* and *Sorbus aucuparia*, along with *Phlyctis argena* on *Betula pubescens*. The taxon *Lecanora chlarotera* was also recorded by the author on *Betula pubescens* within the Scots pine woodland on the adjacent island of Eilean Ban.

The broad-leaved deciduous trees on the Morar archipelago also exhibit at least eight epiphytic lichen taxa which are cited in the Revised Index of Ecological Continuity (Table V *in* Rose, 1976). These Index lichen taxa are represented by *Haematomma elatinum, Lobaria laetevirens, L. pulmonaria, L. scrobiculata, Nephroma laevigatum, Parmelia crinita, Parmeliella tryptophylla* and *Sticta sylvatica.*

The results of the application of the Revised Index of Ecological Continuity by the author to field data from ant Eilean Meadhoin (Rose, 1977b) and Eilean a'Phidhir (Rose, 1977c) are indicated in Table 20.

The application of the Revised Index of Ecological Continuity (Rose, 1976) to Scots pine woodland sites is unconventional in view of its intended use in broad-leave deciduous woodland. Index values arising from this application may, therefore, prove invalid and difficult to interpret. Nevertheless, the stands of Scots pine on the Morar archipelago exhibit a wide range of broad-leaved deciduous trees, in common with other stands in oceanic regions of Scotland. Therefore, ecological continuity of high tree cover may be indicated by Index lichen taxa which occur on the broad-leaved deciduous trees within these stands of Scots pine.

A further consideration relates to the use of *Lobaria* species in the Revised Index of Ecological Continuity. In western Scotland, lichens of the genus *Lobaria* are not restricted to old woodland trees. Indeed, they can readily colonize young trees within recent plantations of broad-leaved deciduous trees. Consequently, the presence of *Lobaria* species *per se* may not necessarily be indicative of ecological continuity of high tree cover. However, in the case of the woodland on the Morar archipelago, various host trees support a range of index lichen taxa, in addition to species of *Lobaria*. The range of index lichen taxa recorded on various host trees on an-t Eilean Meadhoin (Rose, 1977b) is indicated in Table 21.

A distinctive element of the epiphytic lichen flora on an-t Eilean Meadhoin and Eilean a'Phidhir, comprises lichen taxa which are considered by Rose (1977d) as characteristic of relict Scots pine woodland in Scotland. This group of lichens includes *Buellia schereri, Haematomma caesium, H. elatinum* and *Parmeliopsis hyperoptera.* Significantly, these taxa were all recorded on *Pinus sylvestris* (Rose, 1977b, 1977c). The taxa *Buellia schereri* and *Haematomma elatinum* are also cited as possible old forest indicators, and faithful species of Scottish Boreal coniferous forest (Rose, 1976).

Although the majority of epiphytic lichen taxa recorded on the Morar archipelago by Rose (1977b, 1977c) are also represented in broad-leaved deciduous woodland near Kinsadel-Lochan a'Chleirich, there are two taxa represented by *Buellia schereri* and *Parmeliopsis hyperopta,* which appear to be restricted to the Morar archipelago. Significantly, these lichen taxa were both recorded on *Pinus sylvestris* host trees on an-t Eilean Meadhoin and Eilean a'Phidhir (Rose, 1977b, 1977c). The presence of these epiphytic lichens, in conjuction with other possibly faithful species of Scottish Boreal forest, e.g. *Haematomma elatinum* (Rose, 1976) complements the similarities between the Scots pine woodland communities on the Morar archipelago and the remanent Scots pine communities of oceanic districts in western Scotland.

To conclude, the Revised Index of Ecological Continuity (Rose, 1976) provides a useful method of calculating, approximately, the continuity of high tree cover in a broad-leaved deciduous woodland site. This Index is based upon the presence of lichen taxa which are known to be associated with ancient forest areas, and which also exhibit a widespread geographical distribution (Table V in Rose, 1976). Furthermore, this Index also takes into account the effect of regional and

Table 20 - The Revised Index of Ecological Continuity values for woodland on the Morar archipelago, Loch Morar

Site	Index lichen taxon	Revised Index value (n/20 x 100)
an-t Eilean Meadhoin	*Haematomma elatinum* *Lobaria laetevirens* *L. pulmonaria* *L. scrobiculata* *Parmelia crinita* *Parmeliella tryptophylla* *Sticta sylvatica*	35
Eilean a'Phidhir	*Haematomma elatinum* *Lobaria laetevirens* *L. pulmonaria* *L. scrobiculata* *Nephroma laevigatum*	25

Source: derived from data by Rose (1977b, 1977c)

Table 21 - Host trees exhibiting Index lichen taxa on an-t Eilean Meadhoin, Loch Morar

Host tree	Lichen taxon
Betula pubescens	*Haematomma elatinum, Lobaria pulmonaria, L. scrobiculata, Parmelia crinita*
Populus tremula	*Haematomma elatinum, Lobaria pulmonaria, L. scrobiculata, Parmelia crinita, Sticta sylvatica*
Sorbus aucuparia	*Lobaria laetevirens, L. pulmonaria, L. scrobiculata, Parmelia crinita, Sticta sylvatica*
Pinus sylvestris	*Haematomma elatinum, Parmelia crinita*
Taxus baccata	*Lobaria pulmonaria*
Quercus sp.	*Lobaria pulmonaria, Parmeliella tryptophylla*

Source: derived from data by Rose (1977b) climatic variations in lichen species representation at a particular site. An Index value is calculated as a proportion of these lichen taxa (up to a maximum of 20) which occur within a particular woodland site.

Significantly, a number of broad-leaved deciduous woodland sites in Inverness-shire and Ross-shire (Rose, 1977a) have revised index values above 50, indeed, some have far higher values. The Kinsadel-Lochan a'Chleirich woodland, near Loch Morar, has the maximum attainable Index value of 100. Furthermore, the epiphytic lichen flora from this site also exhibits a range of lichen taxa which are cited as "faithful" to old hardwood forests in lowland Britain (see Table III in Rose, 1976).

The author suggests that the Kinsadel-Lochan a'Chleirich woodland, and by association the principal areas of broad-leaved deciduous woodland surrounding Loch Morar, represent mature or old stands of oak or mixed-oak high forest which have been relatively undisturbed over a very long period, with ecological continuity of high tree cover and micro-climate, apart from areas where the forest trees have been subjected to coppicing, and where consequent periodic desiccation has occurred.

A view of mature oak trees near Bracorina, North Morar is illustrated in Plate 9.

The coniferous Scots pine woodland on the Morar archipelago exhibits an epiphytic lichen flora, which shares a number of similarities with the flora of Scots pine woodlands in oceanic districts of western Scotland. The epiphytic lichen flora also exhibits lichen taxa which are considered to be characteristic of remanent Scots pine woodland in Scotland (Rose, 1977d), while *Pinus sylvestris* trees on the islands also host lichen taxa which are cited as possible "faithful" species of Scottish Boreal forest (Rose, 1976).

The author suggests that the island archipelago in Loch Morar supports remanent indigenous Scots pine woodland, which has been relatively undisturbed over a very long period, with ecological continuity of high tree cover, apart from areas where the forest trees have been felled.

In the following chapter aspects of the history of the woodland cover are discussed in the light of the author's investigation of the sedimentary record from the Morar Basin.

Plate 9 Mature native oak trees near Bracorina, North Morar

CHAPTER 5

THE PALAEOLIMNOLOGY AND PALAEOMAGNETIC RECORD FROM THE MORAR BASIN

The sedimentary record of the Morar Basin was investigated by the author with the aim of elucidating aspects of the palaeoenvironment and palaeolimnology, concentrating principally upon the palaeomagnetic record and microscopic fossil plant remains preserved in the bottom sediments of Loch Morar. Two long cores of sediments were obtained from beneath *circa* 61metres of water at the western end of Loch Morar (National Grid reference: NM 780 900) with a Mackereth pneumatic corer (Mackereth, 1958).

The sediment cores were sampled and measured for their natural remanent magnetism (nrm), including the palaeomagnetic secular variation, magnetic intensity and magnetic susceptibility. The palaeomagnetic analyses and data provided a method of dating the sediment cores from Loch Morar.

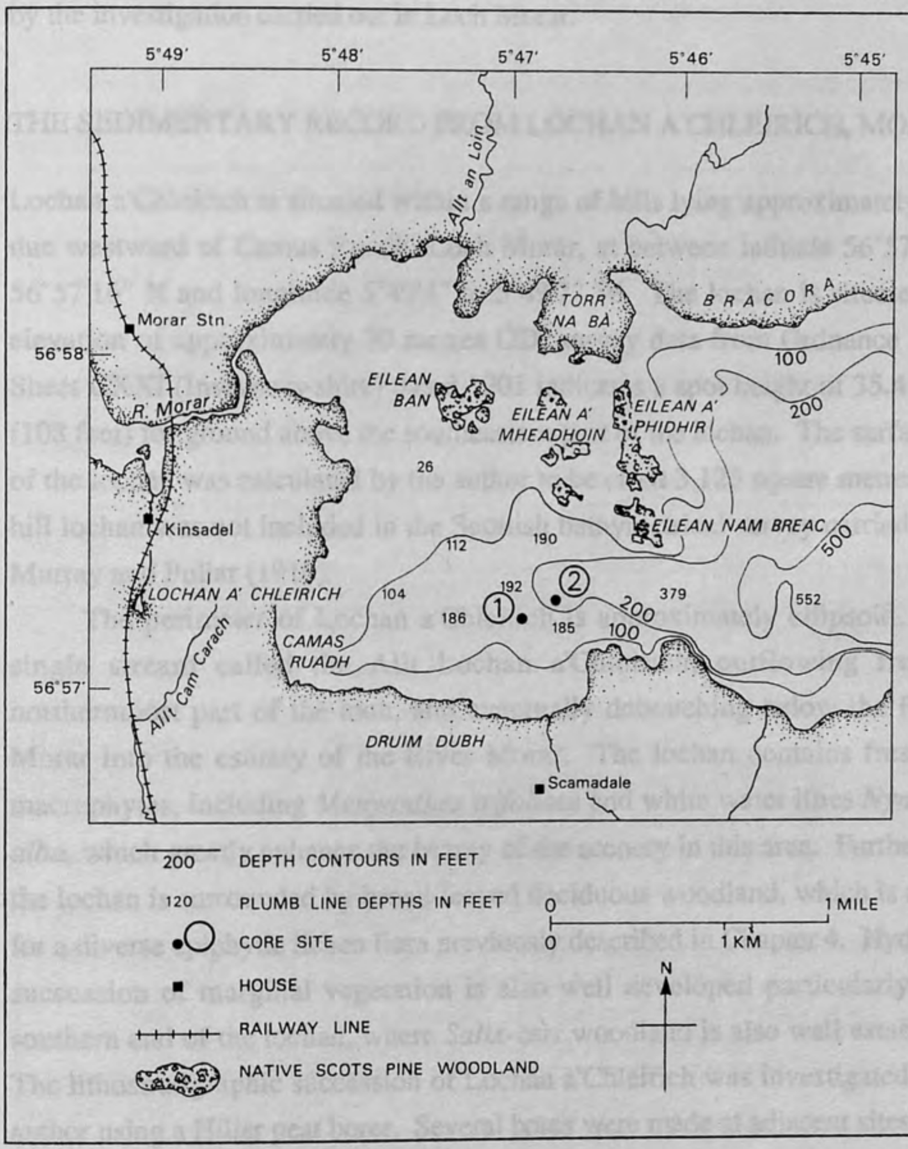
The lithostratigraphy of the sediment cores was recorded using a method modified from Troels-Smith (1955). In addition, a composite photographic record was made of the upper 105 centimetres of sediment core 2.

The sedimentary sequence of the upper part of the long cores was found to be best preserved in sediment core 2, therefore this core was selected by the author for microscopic analysis of fossil diatoms (Class Bacillariophyceae) and fossil tree pollen. These analyses and data provided new information about the history of the woodland cover in the Morar Basin during the Holocene Epoch, *sensu* Harland *et al.* (1989) *circa* 10,000 years BP to present, while also providing an independent chronological verification of the palaeomagnetic secular variation record.

On the basis of chronological data derived from the analyses of core 2, a mathematical model was formulated to define the chronology of the upper part of the sedimentary succession from Loch Morar. The range of analytical techniques and the data arising from their application to the sediment cores from Loch Morar are described and discussed in this chapter.

The investigation of the sedimentary record of the Morar Basin was not wholly confined to the bottom sediments of Loch Morar. Indeed, the author also examined a small hill lochan called Lochan a'Chleirich (National Grid reference: NM 678 913), situated adjacent to Loch Morar. The location of Lochan a'Chleirich and the Mackereth core sites at the western end of Loch Morar are indicated in Figure 10.

Fig.10 THE WESTERN PART OF LOCH MORAR AND THE LOCATION OF THE CORE SITES



Source: Murray & Pullar (1910)

Lochan a'Chleirich is situated within a range of hills which separate the western end of Loch Morar from the coast and the Sound of Sleat. The author's investigation of this lochan revealed the existence of fossil marine invertebrates preserved within a distinctive tripartite sediment sequence, which is interpreted as representing the Late Devensian Lateglacial sedimentary record in the Morar Basin. The sedimentary succession from this site is described below, followed by the investigation carried out in Loch Morar.

THE SEDIMENTARY RECORD FROM LOCHAN A'CHLEIRICH, MORAR

Lochan a'Chleirich is situated within a range of hills lying approximately 930m due westward of Camus Ruadh, Loch Morar, at between latitude 56°57'12" to 56°57'16" N and longitude 5°49'4" to 5°49'7" W. The lochan is situated at an elevation of approximately 30 metres OD; survey data from Ordnance Survey Sheet CXXI (Inverness-shire) dated 1901 indicates a spot height of 35.4 metres (108 feet) for ground above the southeastern part of the lochan. The surface area of the lochan was calculated by the author to be *circa* 3,125 square metres. This hill lochan was not included in the Scottish bathymetrical survey carried out by Murray and Pullar (1910).

The perimeter of Lochan a'Chleirich is approximately ellipsoid, with a single stream called the Allt Lochan a'Chleirich, outflowing from the northernmost part of the loch, and eventually debouching below the Falls of Morar into the estuary of the River Morar. The lochan contains freshwater macrophytes, including *Menyanthes trifoliata* and white water lilies *Nymphaea alba,* which greatly enhance the beauty of the scenery in this area. Furthermore, the lochan is surrounded by broad-leaved deciduous woodland, which is notable for a diverse epiphytic lichen flora previously described in Chapter 4. Hydroseral succession of marginal vegetation is also well developed particularly at the southern end of the lochan, where *Salix*-carr woodland is also well established. The lithostratigraphic succession of Lochan a'Chleirich was investigated by the author using a Hiller peat borer. Several bores were made at adjacent sites within close proximity to the northernmost part of the lochan, upon an area of hydroseral vegetation situated a few metres eastward of the stream called Allt Lochan a'Chleirich. The lithostratigraphic succession at Lochan a'Chleirich is indicated in Table 22, and summarized in schematic form with accompanying notes in Table 23.

The succession is notable for a distinctive tripartite sequence of sediments which is overlain by several metres of *Sphagnum* peat. The tripartite sequence

Table 22 - Lithostratigraphic record from Lochan a'Chleirich, near Morar

Bore I

Depth below surface (m)	Description
0-5.675	Brown peat; fragmented wood at 4.775m
5.675-5.975	Grey-brown peat with twigs and fragments of wood
5.975-6.215	Brown peat
6.215-6.235	Transition
6.235-6.920	Brown-green mud with fine plant remains
6.920	Transition
6.920-6.975	Green-brown mud with fine fragments of mica schist

Bore II

Depth below surface (m)	Description
6.825-6.845	Dark brown-green mud with fine plant remains
6.845-6.865	Transitional; grey-brown silt with sand
6.865-6.905	Grey sand
6.905-6.940	Light grey clay
6.940-6.965	Light grey to grey-brown clay with finely scattered plant remains
6.965-6.970	Transition
6.970-7.125	Brown-green mud with numerous plant remains

Bore III

Depth below surface (m)	Description
6.935-6.945	Dark grey clay with fine fragments of mica-schist
6.945-6.950	Transition
6.950-7.155	Green-brown mud with numerous plant remains
7.155-7.160	Transitional; grey clay with sand
7.160-7.390	Grey clay; dark grey clay at between 7.305 and 7.390m
7.390	Transition
7.390-7.405	Olive-grey clay with some silt and very fine fragments of fossil shells
7.405	Transition
7.405-7.570	Light grey clay matrix with numerous fossil molluscan shells, barnacle plates and fine gravel
7.570-7.605	Light grey clay with scattered fragments of fossil molluscan shells and some fine gravel

Bore IV

Depth below surface (m)	Description
7.675-7.810	Grey clay with numerous fossil molluscan shells, barnacle plates and fine gravel
7.810-7.825	Light grey clay with fine fragments of fossil shells and fine gravel
7.825-7.975	Light grey thixotropic clay; white to light grey laminae, with a pink hue in oblique view at 7.878-7.883m and 7.895-7.900m
7.975	Fine fragments of white quartzite
8.000	Inferred bedrock and base of the sedimentary succession

rests upon Moine schist bedrock, and comprises a basal minerogenic sediment containing marine invertebrate fossils, which is succeeded in turn by a predominantly organic lacustrine sediment (measuring at least 20 centimetres in depth), and a minerogenic sediment (measuring at least 10 centimetres in depth). The tripartite sequence is overlain by accumulated peat measuring at least 6.8 metres in depth.

THE LITHOSTRATIGRAPHIC RECORD FROM LOCHAN A'CHLEIRICH, MORAR

The lithostratigraphic succession at Lochan a'Chleirich is interpreted by the author as representing Late Devensian Lateglacial sediments which are overlain by Holocene peat and predominantly organic lacustrine sediments. Indeed, the succession closely parallels the descriptions of sedimentary sequences recorded from many locations in northwestern Europe, which have been attributed to the Late Devensian Lateglacial (Lowe and Walker, 1984). Palaeobotanical evidence from such sites suggests that the basal minerogenic member of the tripartite sequence accumulated immediately following deglaciation of the Late Devensian ice, while the intervening predominantly organic sediment contains a fossil record derived from vegetation dominated by shrub or woodland which developed in the landscape during the period of climatic amelioration associated with the Late Devensian Lateglacial Interstadial. The upper minerogenic member of the tripartite sequence accumulated during the cold phase of the Loch Lomond Stadial/Younger Dryas, at which time a severe periglacial regime prevailed in the catchment area of the lake basins situated beyond the limit of the glacier ice; surrounding slopes were affected as much by freeze-thaw activity and solifluction as by overland flow processes. Significantly, lake basins which were occupied by glacier ice during the Loch Lomond Stadial have not revealed the Lateglacial tripartite sequence of sediments; it is reasonably argued that earlier sedimentary evidence at sites affected by Loch Lomond Stadial glaciers would have been destroyed as a direct result of erosion by glacier ice.

A schematic representation of the lithostratigraphic succession at Lochan a'Chleirich is presented in Table 23.

Table 23 - A schematic representation of the lithostratigraphic succession at Lochan a'Chleirich, indicated by Hiller bore data from the northern part of the lochan

Description	*Regional and local developments*
Sphagnum peat with occasional layers of macro-fossil wood	Hydroseral vegetation in the littoral zone of the lochan and the development of predominantly fragments broad leaved deciduous woodland cover in the catchment area
Predominantly organic green-brown lacustrine mud with fine plant remains	Climatic amelioration associated with the start of Holocene Epoch at 10,000 years BP
Predominantly minerogenic grey clay with sand	Climatic deterioration associated with the Loch Lomond Stadial between *circa* 11,000 to 10,000 years BP Solifluction in the catchment area
Predominantly organic green-brown lacustrine mud	Development of Late Devensian Lateglacial Interstadial vegetation cover in the catchment area
Sand and grey clay	Relative sea-level fell rapidly between *circa* 13,000 to 12,000 years BP Cessation of maritime influence in the lochan
	Melting glacier ice in response to climatic amelioration, and marine incursion into the lochan
Grey clay and fine gravel with marine invertebrate fossils	Deposition *in situ* of marine sediments analagous with the Clyde Beds Formation *sensu* Jamieson (1865)
Thixotropic grey clay with fine laminations	Late Devensian glaciation ended between *circa* 14,000 to 13,000 Years BP

Samples of sediment containing marine invertebrate fossils were forwarded to Dr J.D. Peacock of the British Geological Survey (Edinburgh) who kindly provided information about the fossil fauna, which is presented below.

THE MARINE INVERTEBRATE FOSSILS FROM LOCHAN A'CHLEIRICH, MORAR

The fossil fauna from Lochan a'Chleirich contained representatives of the following taxonomic groups:-

Family Littorinidae	*Littorina obtusata, L. rudis*	periwinkles
Family Anomiidae	*Hereranomia squamula*	bivalve mollusca
Family Acmaeidae	*Acmeae* ref. *virginea*	limpets
Family Mytilidae	*Mytilus* sp.	mussels
Family Balanidae	*Balanus* sp.	barnacles
Family Echinidae	*Echinus* sp.	sea urchins

The identifiable fossil fauna comprise taxa which are represented in the current British marine fauna. Moreover, they exhibit a wide geographical distribution, with some taxa, e.g. *Littorina* spp. occurring as far north as the White Sea, northern Siberia.

Current representatives of the fossil taxa suggest that the fossil fauna from Lochan a'Chleirich occupied a shallow marine environment, which ranged from low in the intertidal zone down to a few metres depth in the sea. While it is possible that some of the fossils may have been transported into the lochan, there is no evidence that the fragments have been significantly rounded by wave action. Therefore, it seems reasonable to assume that the fossils represent a predominantly *in situ* marine fauna at this site.

A number of *Littorina* spp. shells exhibited bores attributed to the serpulid annelid *Polydora* sp., while some fragmented shells suggested that some of the fauna were probably bored by natural predators, e.g. the prosobranch mollusca *Lunatia (Natica* auct.) spp. and broken on the sea floor; representatives of the genus *Lunatia* occur in the depth range from the lower shore down to the low water mark. Although current British *Littorina* spp. occur predominantly within the intertidal zone, they can nevertheless actively migrate to deeper water. Indeed, *Littorina* spp. have been recorded from Murmansk, occurring in sea-water of several metres depth during winter, while in eastern North America this genus has been recorded occurring on the sea floor of coastal waters. In the high Arctic *Littorina* spp. are unable to live within the inter-tidal zone because of drifting sea ice, therefore, their active migration to deeper water may reflect a response to colder surface water conditions.

The existence of an inferred Late Devensian Lateglacial sedimentary record at Lochan a'Chleirich is significant in relation to the postulated limit of Loch Lomond Stadial glacier ice in the Morar Basin. Indeed, the limit is postulated to have been in the vicinity of the present western shore of Loch Morar (Peacock, 1970), which is situated approximately 1.6 kilometres distance eastward of Lochan a'Chleirich.

The sedimentary record from Lochan a'Chleirich is also significant in relation to the relative sea-level height in the Morar Basin during the Late Devensian Lateglacial period. Indeed, the presence of apparently *in situ* marine invertebrate fossils within clay and fine gravel of the basal member of the tripartite sequence of sediments, strongly suggests that the lochan was formerly in direct physical communication with the sea, following deglaciation of the Late Devensian ice, dating from perhaps shortly after 13,000 years BP. Although Lochan a'Chleirich is presently situated at an approximate elevation of 30 metres OD, at the time of marine inundation immediately following the Late Devensian glaciation, the site would have been substantially depressed below its present elevation as a result of glacial isostasy. Estimates of relative sea-level at this time place it at *circa* 41 metres below OD (Peacock, 1970). Raised beaches comprising sloping terraces of sand and gravel attributed to the Late Devensian Lateglacial reach a levelled height of *circa* 41 metres OD, and possibly up to *circa* 46 metres OD, between Arisaig and Morar (Peacock, 1970). Thus, the site must have been depressed by this amount.

The basal member of the tripartite sequence of sediments, comprising clay with fine gravel and marine invertebrate fossils, closely parallels the description of the Clyde Beds Formation *sensu* Jamieson (1865), which has been reported from a number of coastal localities in western Scotland, including Loch Linnhe and Fort William (Jamieson, 1865).

THE SEDIMENTARY RECORD FROM LOCH MORAR

CORING TECHNIQUE

Given the case that it is very easy to disturb and deform the structure of sediments in lakes during coring, there are considerable advantages in using a corer which penetrates the bottom sediments at a rate which is both slow and controllable. Indeed, these features are embodied in the pneumatically powered corer developed by Mackereth (1958). Furthermore, this device has proven particularly suitable for collecting sediment cores in an appropriate condition for palaeomagnetic sampling and analysis, provided that the water depth of the coring site does not exceed more than *circa* 100 metres (Creer, 1982). The Mackereth corer is also available with a locking device to prevent the core tube twisting relative to the anchor chamber; in large deep lakes there is a tendency for the core tube to gyrate as it penetrates downward into the bottom sediments, thus introducing a long wavelength twist and also breaks in the cores sediments (Creer, 1982).

A Mackereth corer fitted with a replaceable PVC core liners (measuring 6 metres in length and 76 millimetres internal diameter) was used to collect bottom sediments from two selected sites in the western part of Loch Morar.

COLLECTION OF SEDIMENT CORES FROM LOCH MORAR

Two sites were selected by the author for deployment of the Mackereth corer in Loch Morar, on the basis of data from an unpublished sub-bottom reflection survey, kindly provided by Adrian Shine, of the Loch Ness and Morar Project, and complementary data from a bathymetrical survey map compiled by Murray and Pullar (1910).

A sub-bottom reflection survey (Shine, 1976) carried out in Loch Morar using a low frequency sonar has revealed that the bottom sediments at the western end of the loch probably exceed 20 metres in vertical thickness. Furthermore, the sedimentary sequence in this area also appears to exhibit horizontal stratification.

Potential coring sites were therefore selected by the author in an area situated near the western end of the loch, where the bathymetrical contours are relatively widely spaced and the water depth is sufficiently deep to effect the successful operation of a Mackereth corer. The locations of the selected coring sites are indicated in Figure 10. Both sites are close to the depth contour for 200 feet (i.e. 61 metres) thereby largely avoiding the effect of surface wave action on the bottom sediments. Furthermore, these sites are sufficiently deep, with gentle gradients, and distant from turbulent streams discharging into the loch. In point of fact, the availability of sites which fulfilled these criteria coupled with the practical requirements associated with the recovery of long sediment cores, proved to be extremely limited in Loch Morar.

Two long cores of sediments, measuring *circa* 4.75 metres in length and 76 millimetres diameter were obtained from beneath 61 metres of water at the western end of Loch Morar. The cores were collected with a Mackereth corer (Mackereth, 1958) at two locations indicated in Figure 10. Sediment core 1 was obtained at National Grid reference: NM 700 911, while sediment core 2 was obtained at National Grid reference: NM 701 912. Both core sites are located due

Plate 10 Loch Morar and the island archipelago, looking due east from hills near Camus Ruadh

southwestward of the Morar archipelago and separated from each other by a distance of 187.5 metres (615 feet). A view of the Morar archipelago and the region of the loch from which the sediment cores were collected is illustrated in Plate 10.

PREPARATION OF THE SEDIMENT CORES

The two 6 metre long PVC core liners, containing the sediment cores from Loch Morar, with preserved azimuthal directions inscribed on the outer cover of the PVC, were cut with a hacksaw into two sections of approximately equal length on the shore of the loch prior to their transportation by road to Edinburgh. Sediment core 1 was cut at 2.155 metres, while sediment core 2 was cut at 1.935 metres. In both cases, a 1 centimetre length of sediment was removed from the cut ends of the cores, to eliminate any contaminating material accidentally introduced by sawing, and to remove sediment from a zone affected by mechanical disturbance arising from the sawing. The ends of the core sections were then capped and sealed prior to transportation.

The sediment cores were subsequently analysed by the author at the Palaeomagnetic Laboratory of the Department of Geophysics, University of Edinburgh. The facilities for the collection of the cores and subsequent laboratory analysis of the sediments were generously provided by Professor Kenneth M. Creer, Head of the Department of Geophysics, University of Edinburgh.

PREPARATION OF THE SEDIMENT CORES FOR PALAEOMAGNETIC ANALYSIS AND DESCRIPTION OF THE LITHOSTRATIGRAPHIC SUCCESSION

The core sections containing sediment from Loch Morar were carefully cut longitudinally in the laboratory with a circular saw, avoiding undue physical disturbance to the encased sediment. After removal of one longitudinal half of the PVC core liner, the exposed sedimentary sequence was carefully cleaned with a palette knife, avoiding contamination of the sediment sequence with material from adjacent horizons down the core. The cleaned sediment profiles were examined in visible light and a lithostratigraphic record was compiled for both cores. The top of each sediment core was assigned as zero depth, i.e. 0 centimetres in the lithostratigraphic succession. This datum was qualitatively defined as representing the approximate water-sediment interface in the sediment column.

THE LITHOSTRATIGRAPHY OF THE SEDIMENT CORES FROM LOCH MORAR

The sediment lithostratigraphy of both cores was described using a modified method based upon a procedure devised by Troels-Smith (1955). Particular importance was attached to the following criteria:-

(i) *Colour* - the moist sediment was described according to the principles of the Munsell Soil Colour Charts (1954)

(ii) *Contact* - the nature of the contact between different sediment types was examined and described as either sharp or irregular, with abrupt or gradual transitions

(iii) *Stratification* - the sediment profile was examined for homogeneity and stratification of the sediment types

(iv) *Structure and texture* - the texture of the sediment types was qualitatively determined by touch: granular and rough corresponding to sand particles; smooth and silk-like corresponding the silt particles; malleable and plastic in the wet state corresponding to clay particles. These definitions correspond with a quantitative assessment of the size range of the mineral particles according to the Wentworth particle-size scale, i.e. sand (0.0625-2mm), silt (0.004-0.0615mm), clay (<0.004mm) as defined by Wentworth (1922).

The lithostratigraphic record of sediment cores 1 and 2 from Loch Morar are presented in Tables 24 and 25 respectively. A summary of the Munsell colour notations that were used in the lithostratigraphic descriptions is presented in Table 26. A photographic record of the upper 105 centimetres of sediment core 2 is illustrated in Plate 11. The author was kindly assisted in the photography of this core by Dr Andrew Sandford, University of Edinburgh.

Sediment core 1 penetrated the bottom sediments in Loch Morar to a depth of 477.5 centimetres, while sediment core 2 penetrated the bottom sediments to a depth of 485.8 centimetres.

Table 24 - Lithostratigraphic record of Loch Morar sediment core 1

Depth down core (cm)	Description
0-5.0	Dark brown/brown lacustrine mud (7.5YR4/4-3/2) Gradational contact
5.0-6.0	Grey brown/light olive brown silt (2.5Y5/2-4) Sharp contact
6.0-10.0	Dark brown/red Iron (III) Oxide in parallel laminations (7.5YR3/2-2.5YR5/8) with brown/strong brown lacustrine mud (7.5YR5/4-6). Gradational contact
10.0-20.0	Brown/strong brown lacustrine mud matrix (7/5YR5/4-6) with dark brown Iron (III) Oxide (7/5YR3/2) tending to red (2/5YR5/8) at lower boundary. Sharp contact
20.0-30.0	Light yellow brown lacustrine mud (2.5Y6/4) with light yellow brown silt (10YR6/4) in parallel laminations Scattered dark brown particles (7/5YR3/2) ref. Iron (III) Oxide, between 22.5-23.5cm. Sharp contact
30.0-30.5	Light brown grey silt (2.5Y6/2). Sharp contact
30.5-39.0	Grey brown to light olive brown silt with fine sand (2.5Y5/2-4). Sharp contact
39.0-66.5	Light yellow brown clay with silt (2.5Y6/4) and fine sand in thin parallel laminations. Sharp contact
66.5-80.0	Alternate grey and olive grey clay with silt (5Y5/1 and 5Y5/2) in parallel laminations. Gradational contact
80.0-83.0	Very dark grey to grey fine sand with clay (5Y3/1). Gradational contact
83.0-90.5	Very dark grey to grey sand (5Y3/1). Normal grading Sharp contact
90.5-94.0	Grey clay with fine sand (5Y5/1). Regular bedding Sharp contact
94.0-127.5	Grey clay (5Y5/1) with fine sand in irregular layers Gradational contact
127.5-477.5	Grey to dark Grey to very dark grey thixotropic clay with silt and occasional layers of sand (5Y5/1-5Y4/1-5Y3/1)
	The base of the sedimentary succession in Loch Morar was not encountered in the sediment core

Table 25 - Lithostratigraphic record of Loch Morar sediment core 2

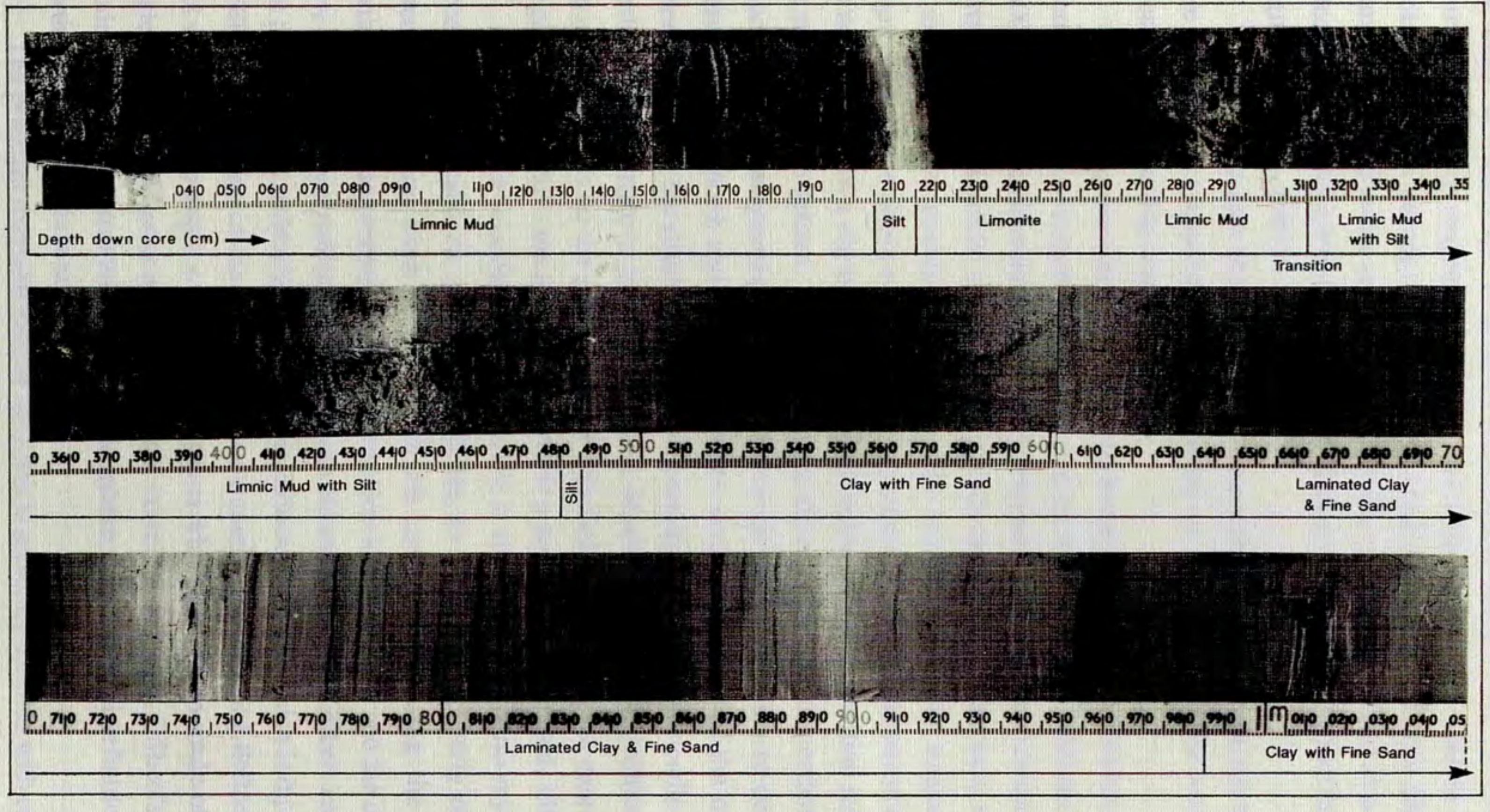
Depth down core (cm)	Description
0-20.5	Dark brown/brown lacustrine mud with occasional particles of mica schist (7.5YR4/4-2). Gradational contact
20.5-20.8	Pale yellow silt with some clay (5Y7/3). Gradational contact
20.8-21.5	Light olive brown silt (2.5Y5/4). Gradational contact
21.5-26.0	Dark brown/brown Iron (III) Oxide in parallel laminations (7.5YR3/2-4/2) with dark brown/brown lacustrine mud (7/5YR4/4). Gradational contact
26.0-31.0	Dark brown/brown lacustrine mud (7.5YR4/4) with occasional dark brown/brown Iron (III) Oxide (7.5YR3/2-4/2) Gradational contact
31.0-48.0	Light olive brown lacustrine mud (2.5Y5/4-5/5) with yellow brown silt (10YR5/5) in parallel laminations Scattered fine black particles ref. Magnetite (γ-Fe_2O_3) between 37.5 and 31.0cm. Sharp contact
48.0-48.5	Yellow brown silt (10YR5/6). Sharp contact
48.5-48.7	Light grey clay with silt (2.5Y7/0). Gradational contact
48.7-64.5	Grey to light grey clay with silt and fine sand (5Y6/1) tending to light olive grey (5Y6/2). Normal grading, i.e. with increasing silt and fine sand towards the lower boundary. Thin laminations of sand between 62.0 and 64.5cm. Sharp contact
64.5-98.5	Alternate olive and grey to light grey clay with fine sand (5Y5/3-5Y6/1) in parallel laminations; 40 laminae between 70.0 and 80.5cm. Gradational contact
98.5-105.5	Grey to light grey clay with thin quasi-parallel laminations of sand (5Y6/1). Woody plant fragments at 101cm Sharp contact
105.5-120.0	Grey to light grey sand with clay (5Y6/1). Sand between 105.5 and 110cm. Slumped layers of sand between 110 and 117.5cm. Sharp contact
120.0-140.0	Grey to light grey clay (5Y6/1) with several thin layers of sand. Irregular contact
140.0-485.8	Grey to light grey to grey thixotropic clay with silt and occasional layers of sand (5Y6/1-5Y5/1) The base of the sedimentary succession in Loch Morar was not encountered in the sediment core

Table 26 - Colour notations used in the lithostratigraphic description of the sediment cores from Loch Morar

Colour notation	*Qualitative description*
2.5YR5/8	Red
7.5YR3/2	Dark brown
7.5YR4/2	Dark brown to Brown
7.5YR4/4	Dark brown to Brown
7.5YR5/4	Brown
7.5YR5/6	Strong brown
10YR5/6	Yellowish brown
10YR6/4	Light yellowish brown
2.5Y5/2	Greyish brown
2.5Y5/4	Light olive brown
2.5Y6/2	Light brownish grey
2.5Y6/4	Light yellowish brown
2.5Y7/0	Light grey
5Y3/1	Very dark grey
5Y4/1	Dark grey
5Y5/1	Grey
5Y5/2	Olive grey
5Y5/3	Olive
5Y6/1	Grey to Light grey
5Y6/2	Light olive grey
5Y7/3	Pale yellow

Source: Munsell Soil Colour Charts (1954)

Plate 11: THE SEDIMENTARY SUCCESSION OF CORE 2 FROM LOCH MORAR (0 TO 105cm DEPTH)



THE PALAEOMAGNETIC RECORD FROM THE MORAR BASIN

HISTORICAL INTRODUCTION

The study of magnetism originated from observations of the behaviour of naturally occurring magnetic minerals. As early as the fifth century BC the Ancient Hellenic people recorded the mutual attraction between pieces of haematite-bearing rocks (containing α-Fe_2O_3), which were mined in a district called Magnesia, which is now in western Turkey; these rocks became known as magnets (Morgan, 1989).

By the latter part of the Twelfth Century AD natural permanent magnets were employed in compasses for navigational use by mariners; these were called lodestones, i.e. leading stones.

The view that the Earth itself exhibits a magnetic character, which broadly resembles that of a magnetized sphere, was postulated by Dr William Gilbert (1600) in a remarkable treatise entitled *"De Magnete"*. Gilbert demonstrated that a mariner's compass needle which is free to rotate about a horizontal axis, will take up an equilibrium position inclined to the vertical axis. By suspending a magnetized needle above a sphere cut from lodestone, Gilbert demonstrated that the needle assumes a dip angle which varies according to its position relative to the surface of the sphere. Furthermore, he showed that the suspended needle responds to the magnetization of the whole sphere, rather than to centres of attraction at the north and south poles. He used the analogy of the magnetic sphere to explain the relationship between the dip of a compass needle and the Earth. The dip angle or inclination varies depending upon the position of the mariner's compass on the globe. Gilbert concluded that: *"magnus magnes ipse est globus terrestris" - the Earth globe itself is a great magnet* (Serson, 1981).

This concept was remarkable because it attributed a hitherto mysterious force which directed the mariner's compass, to a physical property of global extent, originating from within the Earth and encompassing the planet. Furthermore, it also predated the concept of Gravitational Force and the universal Law of Gravitation published by Sir Isaac Newton (1687). Gilbert envisaged that the Earth was embraced by a magnetic influence or field which is dipolar, i.e. at 90° to the surface of the sphere, with a magnetic equator being defined as the loci where the dip angle is 0°. Measurements which have been made of the dip angle at various latitudes around the Earth, correlate well with Gilbert's elegant model of the Earth resembling a magnetic sphere. This original definition of the Earth's magnetic poles is still valid.

The principal magnetic axis of the Earth is presently inclined with respect to the planet's axis of rotation at an angle of *circa* 17°. Therefore, the geomagnetic poles and magnetic equator do not correspond with the position of their geographical counterparts. Indeed, the difference between the direction of the geographical pole and the geomagnetic pole is defined as an angle termed the magnetic declination (θ), which varies according to the geographical location; magnetic declination is usually described as being either westerly (θ_W), or as easterly (θ_E). A schematic representation of the Earth's magnetic field is illustrated in Figure 11.

The discovery by Oersted (1820) that a compass magnet is affected by an electrical current, demonstrated that electricity and magnetism are interactive physical processes. Experimental research by Michael Faraday between the years 1831-1852, and particularly his concept in 1831 of the Principle of electromagnetic induction, which indicated that a spinning magnet induces an electrical current or electromotive force within a surrounding coiled conductor (Faraday, 1832) provided the basis upon which James Clerk Maxwell (1873) was subsequently able to mathematically integrate the Laws of Electricity and Magnetism into a universal theory of electromagnetism. Thus, an electrical current flowing in a coiled conductor is surrounded by an associated magnetic field and a magnetic moment. The magnetic moment can therefore by effectively defined in terms of electrical currents, and quantified using a system of electromagnetic units.

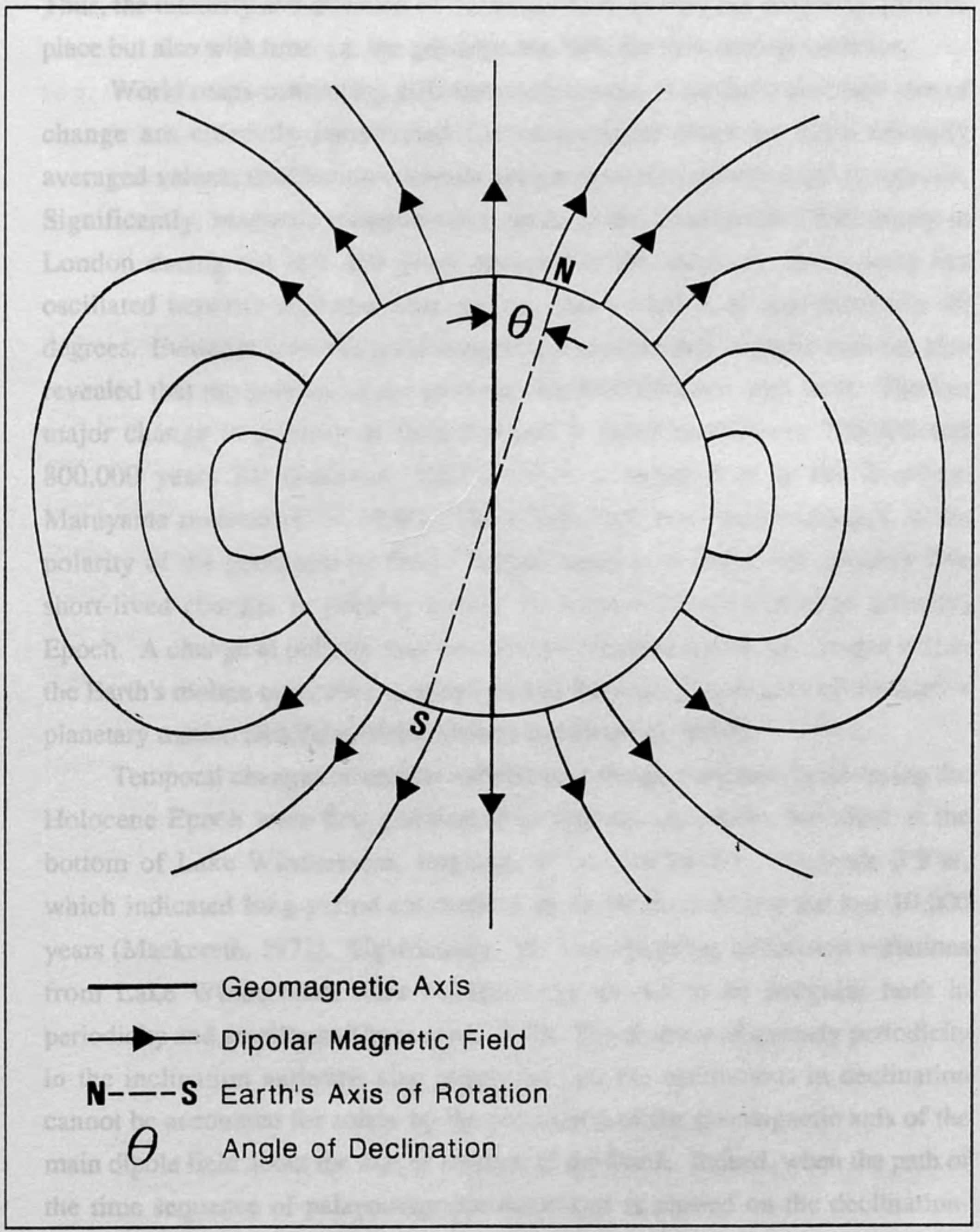
These discoveries led to the development of electronic instrumentation, including magnetometers, which can provide, amongst other things, a method of quantifying and monitoring the Earth's magnetic field.

GEOMAGNETIC SECULAR VARIATION

The Earth's magnetic field originates from complex magneto-fluid processes occurring within the partly molten core of the planet. Seismic wave velocity data suggest that a molten medium, termed the outer core, occurs at between *circa* 2,900 and 5,500 kilometres depth below the crust of the Earth. The molten outer core separates the overlying mantle from the solid inner core. Evidence from meteorites suggests that the core of the planet consists predominantly of iron and nickel; a small proportion of additional elements with a relatively lighter density probably also exist in the molten outer core.

The rotation of the Earth exerts a powerful influence on the symmetry of the geomagnetic field. Indeed, the global field exhibits a strongly axial component; direct measurements of the field at more than 200 magnetic observatories situated around the world have revealed that the symmetry of the field is essentially

Fig.11 SCHEMATIC REPRESENTATION OF THE EARTH'S MAIN-DIPOLE MAGNETIC FIELD



dipolar. However, when the theoretical best-fit of the dipole field is subtracted from the observed field, it is clear that a number of regional anomalies remain, with total magnitudes of about 20 *per cent* of the dipole field. These regional anomalies are collectively referred to as the non-dipole field (Creer, 1982). Significantly, both the dipole and non-dipole parts of the geomagnetic field vary with time, probably as a result of convective movements in the core of the Earth. Thus, the intensity and direction of the magnetic field vary not only from place to place but also with time, i.e. the geomagnetic field exhibits secular variation.

World maps contouring different components of the field and their rate of change are currently constructed for navigational purposes from annually averaged values; declination contours are particularly important for navigation. Significantly, magnetic measurements made at the Greenwich Observatory in London during the last 400 years reveal that the magnetic declination has oscillated between east and west, with a total variation of approximately 40 degrees. Evidence from the palaeomagnetism in rocks and volcanic lava has also revealed that the polarity of the geomagnetic field changes with time. The last major change in polarity or field reversal is dated to between 700,000 and 800,000 years BP (Johnson, 1982), which is referred to as the Brunhes-Matuyama reversal (Cox, 1968). There have also been minor changes in the polarity of the geomagnetic field. Indeed, there is evidence for possibly five short-lived changes in polarity during the current Brunhes (normal polarity) Epoch. A change in polarity may be caused by sudden convection surges within the Earth's molten outer core, perhaps arising from the eccentricity of the Earth's planetary motion (Rikitake, 1966; Melton and Giardini, 1987).

Temporal changes or secular variations in the geomagnetic field during the Holocene Epoch were first discovered in organic sediments deposited at the bottom of Lake Windermere, England, at latitude 54°4'N, longitude 2°9'W, which indicated long-period oscillations in declination during the last 10,000 years (Mackereth, 1971). Significantly, the corresponding inclination variations from Lake Windermere were subsequently shown to be irregular both in periodicity and amplitude (Creer *et al*, 1972). The absence of a steady periodicity in the inclination variation also suggested that the oscillations in declination cannot be accounted for solely by the precession of the geomagnetic axis of the main dipole field about the axis of rotation of the Earth. Indeed, when the path of the time sequence of palaeomagnetic directions is plotted on the declination-inclination plane, it has been observed that both clockwise and counter-clockwise loops are traced out (Creer *et al*, 1972). Furthermore, following the arguments of Skiles (1970), it has been suggested that these observed variations originate from stationary oscillating or pulsating sources in the outer core (Creer, 1977).

The extension of palaeomagnetic studies to various lacustrine sites in northwestern Europe has revealed that the main characteristics of the Lake Windermere record of geomagnetic secular variations (i.e. declination and inclination variations) during the Holocene Epoch can be recognized at sites where sediments of comparable geological age are suitably preserved (Thompson, 1975). Thus, palaeomagnetic studies of lacustrine sediments offer a potential method for regional geological correlation. Furthermore, in situations where conventional dating by radiocarbon assay is deemed to be impracticable (e.g. sediments deposited in oligotrophic lakes often contain very low amounts of organic carbon), the measurement of the palaeomagnetic secular variation record may provide a method of deriving a reliable chronology. This technique was applied by the author to the long sediment cores collected from Loch Morar.

THE PROCESSES OF MAGNETIZATION OF GEOLOGICAL SEDIMENTS

The palaeomagnetic record arises from the collective alignment of small magnetic carriers in the Earth's magnetic field during the course of geological history. In a large number of lacustrine sediments examined to date, the natural remanent magnetization (nrm) is evidently carried by detrital mineral grains of magnetite, which measure less than *circa* 50μm in diameter (Papamarinopoulos *et al.*, 1982). The majority of carriers which contribute to the record are less than 10μm in diameter (Verosub, 1986). The primary magnetic mineral is generally fine grained magnetite, although in certain cases the mineral haematite may be present instead.

The natural remanent magnetization may be acquired in at least three principal ways:-

(1) DEPOSITIONAL REMANENT MAGNETIZATION (drm)

Under typical conditions, the magnetic mineral carriers are weathered by physical or chemical erosion from parent rock and carried by water into a relatively quiet sedimentary environment, where they are deposited as a sediment. Depositional remanent magnetization (drm) may be acquired in calm water as the magnetic carriers descend through the water column. The individual magnetic moments of the carrier grains become preferentially aligned in the direction of the ambient geomagnetic field. When the carrier reaches the interface between the water column and deposited sediment, it has effectively acquired magnetization which reflects the direction of the ambient field at the time of deposition. This depositional remanent magnetization (drm) would accurately represent the behaviour of the geomagnetic field, however, other factors also affect the magnetic carrier both during and after deposition has occurred. These factors include the effect of water currents (Rees, 1961), deposition upon sloping substrata (Hamilton and King, 1964) and upon clearly defined layers at the water-sediment interface, e.g. volcanic tephra, in which case there is a tendency for the magnetic carriers to roll as they reach the substratum (King and Rees, 1966). Indeed, the effect of rolling may account for a net shallowing of inclination, which may amount to at least 10° (King and Rees, 1966). In the majority of situations, however, the water-sediment interface is not clearly defined, usually it represents a transition zone, changing in character from a very dilute dispersion of sediment with a high water content in the upper part and becoming progressively consolidated and de-watered with increasing depth.

Physical disturbance of the magnetic carriers may also occur as a result of the burrowing action of benthic fauna. Indeed, the effect of bioturbation can remobilize the magnetic carriers within the bottom sediment, so that they become re-aligned with respect to the prevailing ambient magnetic field (Ellwood, 1984).

(2) POST-DEPOSITIONAL REMANENT MAGNETIZATION (pdrm)

Post-depositional remanent magnetization (pdrm) may be acquired if the carrier grains are free to rotate in the voids of the sediment matrix; in this situation the carrier grains may respond to secular variations of the geomagnetic field which occur after initial deposition of the sediment. The pdrm process is generally considered to be more important than the former process of magnetization, i.e. drm.

Experimental investigations with synthetic sediments by Tucker (1980) demonstrated that the efficiency of the pdrm magnetization process depends upon the relative diameters of the carrier and bulk carrier matrix grains. The process is most effective in cases where the carrier grains are smaller than the matrix grains. Thus, in a sediment with a high sand content, the magnetic carriers appear to be initially free to rotate in the voids between the relatively larger matrix grains (Payne and Verosub, 1982). Furthermore, the size of the voids decreases progressively as a consequence of compaction; this arises in the natural environment where sediment continues to accummulate *in situ* over a period of time.

The ability of the carrier grains to rotate towards the geomagnetic field direction is progressively impeded as the water content of the sediment matrix decreases. Indeed, when the water content and porosity fall below a critical value, the magnetic carriers become immobile and the magnetization is effectively "blocked in" (Tucker, 1980; Denham and Chave, 1982). An important implication of this process is that the pdrm is acquired over a finite interval of time, where the duration is dependent upon the rate of sediment deposition.

In the case of sediments deposited in lacustrine environments, with typical rates of deposition ranging from *circa* 0.5 to 1 millimetre per year, the "window" through which the geomagnetic secular variations are recorded is *circa* 200 years (Creer and Tucholka, 1982a). Therefore, the magnetization process in lacustrine sediments effectively incorporates a high frequency cut-off filter. In the case of deep ocean sediments, typical rates of deposition are of the order of one hundred times lower than those occurring within lakes. Thus, the recorded palaeomagnetic signal is probably smoothed over intervals of *circa* 20,000 years. Data from laboratory experiments indicate that under conditions where the applied magnetic field strength is similar in order of magnitude to that of the Earth, then the intensity of pdrm is proportional both to the strength of the applied magnetic field, and to the logarithm of the time over which it is applied, providing that the other conditions remain constant (Creer and Tucholka, 1982a). The resolution of the recorded signal is not always effectively realized, however, because of the smoothing associated with the pdrm recording process (Creer and Tucholka, 1982a).

Thus, lacustrine sediments are potentially suitable for recording secular variations with periods of *circa* 10^3 to 10^4 years. At mid-latitudes in the northern hemisphere, the maximum recorded variations in inclination and declination are *circa* 20° and *circa* 40° respectively. Furthermore, these changes have occurred during a time scale of the order of several hundred years (Thompson and Barraclough, 1982). Therefore, by sub-sampling long sediment cores conventionally at 2.5 centimetres consecutive depth intervals, with standard sample boxes, it is possible to sample the geomagnetic secular variation at intervals of several decades, providing that the rate of sediment deposition at the core site has averaged *circa* 0.5 millimetres per year. Furthermore, to obtain a detailed resolution of the angular and temporal parameters, the continuous sequence of closely-spaced samples must be orientated with an uncertainty of less than a few degrees.

(3) CHEMICAL REMANENT MAGNETIZATION (crm)

Sediments may acquire a chemical magnetization (crm) which arises from chemical reduction within the sedimentary environment. Thus, the presence of Iron-reducing bacteria (Chlamydobacteriales) will convert Iron [III] Oxide, or Iron [III] Hydroxide, initially present in the sediment, into Iron [II] Oxide, i.e. magnetite. The newly formed magnetite will acquire a chemical remanent magnetization (crm) in the prevailing ambient geomagnetic field, during the process of crystallization. Thus, in situations where sediments acquire magnetization by this process, the interpretation of the overall remanent magnetization may be complicated.

THE VALIDITY OF LACUSTRINE SEDIMENTS AS RECORDERS OF GEOMAGNETIC SECULAR VARIATION

The validity of lacustrine sediments as reliable recorders of past geomagnetic secular variations is substantiated by the agreement of palaeomagnetic data from Greece, covering the last three to four millenia, with parallel data derived from archaeological artifacts, including pottery and kiln walls (Creer *et al*, 1981; Kovacheva, 1980). Similar agreement has also been obtained for palaeomagnetic data from the United Kingdom with archaeological artifacts (i.e. archaeomagnetic data) and historical data from magnetic observations for northwest Europe, although covering a shorter time interval.

The palaeomagnetic record of lacustrine sediments, moreover, offers the possibility of correlation between different lakes, so that a continuous record can be assembled for a particular geographical region. The archaeomagnetic method, by comparison, can only be applied to a few geographical regions where ancient civilizations have flourished. Furthermore, this technique cannot be extended far beyond the fourth millenium BC (*circa* 6,000 years BP), when the process of baking pottery in kilns appears to have been invented (Creer and Tucholka, 1982a).

Following the pioneering study of geomagnetic secular variation in cores of lacustrine sediments from Lake Windermere (Mackereth, 1971), many data of high resolution have been obtained from various lakes in different geographical regions of the world, particularly from western Europe.

CORRELATION OF INDIVIDUAL PALAEOMAGNETIC RECORDS

The palaeomagnetic records from parallel cores taken from a given lake, can be correlated on the basis of their lithostratigraphy and magnetic susceptibility logs; correlation of data from a wider geographical context, i.e. from different lakes within a geographical region, requires accurate independent dating of individual sediment cores.

Although the radiocarbon method (Libby, 1955) is widely used to obtain absolute ages (determined in radiocarbon years, rather than calendar years), there is a reasonable case for supplementing the radiocarbon assay of lacustrine sediment cores with fossil pollen studies, thereby reducing the possible error arising from the presence of contaminant organic carbon within the sediment. Many cases have been reported where the determined C^{14} ages are systematically erroneous for various reasons (Creer, 1982). Indeed, transformation from the depth scale to a reliable time scale constitutes one of the most difficult problems encountered in the construction of palaeomagnetic secular variation records (Creer and Tucholka, 1982a).

THE CONSTRUCTION OF TYPE-CURVES OF GEOMAGNETIC SECULAR VARIATION FOR A GIVEN GEOGRAPHICAL REGION, WITH PARTICULAR REFERENCE TO WESTERN EUROPE

Palaeomagnetic data from lacustrine sediments deposited during the last 10,000 years BP (i.e. the Holocene Epoch) are available for many areas of Europe, ranging from Greece (Creer *et al*, 1981), Poland (Creer *et al*, 1979), Finland (Thompson and Stober, 1977), Switzerland (Creer *et al*, 1980) and the United Kingdom (Mackereth, 1971; Thompson and Turner, 1979; Turner and Thompson, 1981).

The most comprehensive of the data sets are those from Lake Windermere and Loch Lomond in the United Kingdom. Furthermore, these data have the best dating control. Both data sets were used by Creer and Tucholka (1982a) to construct European type-curves of declination and inclination (Figure 2 in Creer and Tucholka, 1982a) which have been reproduced in Figure 12 by kind permission of these authors.

METHOD OF CONSTRUCTION OF THE EUROPEAN TYPE-CURVES BY CREER AND TUCHOLKA (1982)

The combined data sets from Loch Lomond and Lake Windermere were used for the period dating from the present to *circa* 5,000 years BP, beyond this date only Lake Windermere data were available for use.

The individual core records were re-computed at equal 40-year time intervals, however, before the individual core data could be combined it was necessary to take into account two important factors which are implicated in the coring procedure. Indeed, the sediment cores are rarely, if ever, orientated with the azimuth, and furthermore, one cannot be sure that the coring device penetrates the bottom sediments in the vertical plane, i.e. perpendicular to the sediment substratum. Therefore, some adjustments to the measured palaeomagnetic directions were necessary before the individual core data could be combined. Thus, the mean of the population of unit vectors for each core, for the interval 0 to 8,000 years BP was calculated by Creer and Tucholka (1982a), and together with all the unit vectors, it was rotated into the direction of the axial geocentric dipole field value of *circa* 70° for the region (latitude *circa* 55°N, longitude, *circa* 4°W). The directions were rotated and the amplitudes were normalized before stacking the data and computing standard error bars at each time-horizon. The co-ordinate system was rotated so that the mean declination (D_m) was set to 0° and the mean inclination (I_m) was set to the axial geocentric dipole field value of $I_{AD} = 74°$ positive.

While this procedure cannot orientate the palaeomagnetic records in a perfect manner, given the probability that the secular variations have not actually averaged out over 8,000 years, nevertheless, any error introduced by this procedure will be systematic for a given geographical region. The amplitudes of the individual records were normalized by Creer and Tucholka (1982a) to correct for variations in the efficiency of the magnetization process, the records were adjusted and the normalized data points were then stacked. Finally, standard error bars were then computed by using Fischerian statistics (Creer and Tucholka, 1982a).

The procedure of stacking the data was adopted by Creer and Tucholka (1982a) with the objectives of removing spurious features exhibited by some of the individual records, and to enhance the signal to noise ratio. Significantly, these objectives are invariably achieved when *instrumental* records are stacked, primarily because the time parameter has been measured very accurately. In contrast, the usual chronometric model used to transform palaeomagnetic variation records from depth to time, assumes uniform rates of sediment deposition between the depths of adjacent chronological markers or time-checks (derived from radiocarbon ages or the principal palaeomagnetic features used for correlation), which is not valid; each radiocarbon age determination is subject to a small percentage experimental error. Consequently, stacked records of core data of geomagnetic secular variation often show relatively less fine detail than some of the better quality individual records comprising the stacked data (Creer and Tucholka, 1982a).

Significantly, the validity of constructing type-curves of geomagnetic secular variation for specific geographical regions, is based upon evidence that secular variations are coherent over distances of the order of at least several hundred kilometres, and possibly even a few thousand kilometres (Verosub, 1986). The feasibility of dating geological sediments by correlation of secular variation records and regional type-curves is therefore a reasonable prospect, despite the inherent limitations of the palaeomagnetic record which have been discussed. To date type-curves have been constructed for the following geographical regions:-

(i) Europe (Turner and Thompson, 1981; Creer and Tucholka, 1982a)
(ii) East-central North America (Creer and Tucholka, 1982b; Lund and Bannerjee, 1985)
(iii) Australia (Barton and McElhinny, 1981; Constable and McElhinny, 1985)
(iv) Southern South America (Creer *et al*, 1983)
(v) China (Wei *et al*, 1981)

The type-curves of geomagnetic secular variation for the United Kingdom and western Europe constructed by Creer and Tucholka (1982a) are reproduced with kind permission of these authors in Figure 12. These type-curves illustrate magnetic declination and magnetic inclination, respectively, plotted against a time-scale in radiocarbon years before present (BP).

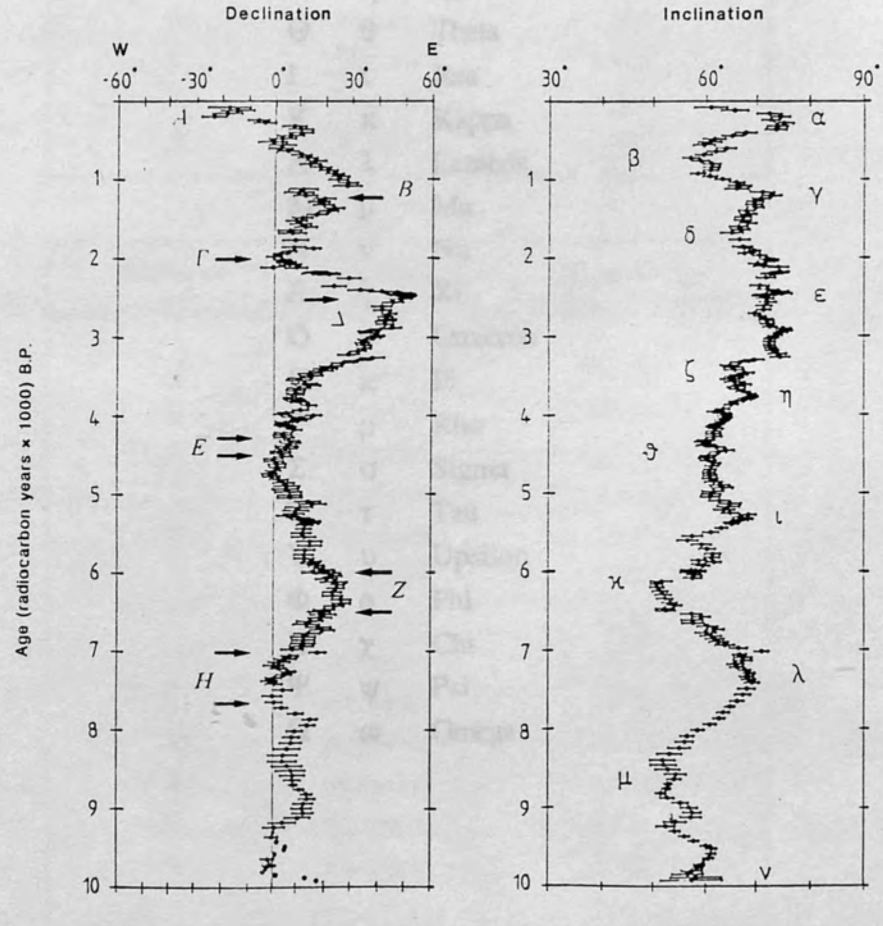
The type-curves of Creer and Tucholka (1982a) reveal that magnetic declination and magnetic inclination vary with amplitudes of about ±10°. The scale divisions of declination and inclination denote increments of 10°. The principal features of the recorded geomagnetic secular variation are labelled by Creer and Tucholka (1982) with capital Greek letters A to H for declination, and lower case Greek letters α to υ for inclination. The Greek alphabet is cited in Table 27. Significantly, the same patterns of secular variation have also been recognized in the palaeomagnetic records obtained from Greece (Creer *et al*, 1981) and Poland (Creer *et al*, 1979), both of which extend back to 6,000 years BP, while the case is also similar for records obtained from Switzerland (Creer *et al*, 1980) which extend beyond the United Kingdom record, to *circa* 14,000 BP, although the dating control is not as good for these regions (Creer and Tucholka, 1982a).

There are some important differences to note between the type curves of Creer and Tucholka (1982a) reproduced Figure 12, with the type-curves compiled by Turner and Thompson (Figure 5, 1981). In the latter case, the authors rotated the co-ordinate system so that the mean declination (D_m), and significantly, the mean inclination (I_m) were both set to 0°. Furthermore, data from Lake Geirionydd (Wales) were included along with data from Loch Lomond and Lake Windermere, while the timescale is presented in calendar years rather than radiocarbon years.

The radiocarbon ages (quoted in uncorrected radiocarbon years BP) which correspond to the principal features of declination and inclination secular variation, indicated in the European type curves *sensu* Creer and Tucholka (1982a) are summarized in Table 28. These data are potentially useful in circumstances where correlation can be made between the type-curves and a record obtained from a particular site under investigation. Moreover, it may also provide, by correlation, useful chronological markers in the geological succession of a site. The amplitude of the individual features of declination and inclination which are recorded at a particular geographical location, depends in particular upon the sensitivity of the sediment to the ambient geomagnetic field, and also upon the rate of sediment deposition. Thus, in situations where the rate of sediment deposition is particularly low, e.g. deep ocean basins, the amplitude of the secular variation record becomes attenuated and effectively smoothed with time. Therefore, it is not necessarily significant if the amplitude of an individual site record does not correspond exactly with the type-curves for the appropriate geographical region.

Extremely high resolution palaeoenvironmental reconstruction can be achieved in situations where correlation is possible between secular variation records. Indeed, if several sites within a geographical region exhibit a depositional remanent magnetization (drm), then specific features exhibited by the individual site records can be used as distinct chronological markers or time-checks in the regional geological succession. Furthermore, where palaeoecological data from fossil pollen and plankton are also available from the geological succession, these can be used to reconstruct the temporal variation in palaeoenvironmental conditions, and in appropriate situations reveal temporal changes in terrestrial vegetation cover. The presence of volcanic tephra layers within the geological succession can also be evaluated. Furthermore, because each tephra has a distinctive geochemistry, the spatial distribution and chronology of volcanic eruptions can also be reconstructed.

Fig.12 TYPE-CURVES OF GEOMAGNETIC SECULAR VARIATION FOR THE U.K.



N.b. Horizontal arrows indicate inferred extremes for the declination features

Source: Creer and Tucholka (1982)

Table 27 - The Greek alphabet

Α	α	Alpha
Β	β	Beta
Γ	γ	Gamma
Δ	δ	Delta
Ε	ε	Epsilon
Ζ	ζ	Zeta
Η	η	Eta
Θ	θ	Theta
Ι	ι	Iota
Κ	κ	Kappa
Λ	λ	Lambda
Μ	μ	Mu
Ν	ν	Nu
Ξ	ξ	Xi
Ο	ο	Omicron
Π	π	Pi
Ρ	ρ	Rho
Σ	σ	Sigma
Τ	τ	Tau
Υ	υ	Upsilon
Φ	φ	Phi
Χ	χ	Chi
Ψ	ψ	Psi
Ω	ω	Omega

Table 28 - Data pertaining to the geomagnetic secular variation in Europe during the Holocene Epoch

Declination Feature Label	Declination (θ_W or θ_E)	European Age (radiocarbon years BP)
A	Westerly	150(m)
B	Easterly	1,200
Γ	Westerly	2,000
Δ	Easterly	2,500
E	Westerly	4,200
Z	Easterly	6,300
H	Westerly	7,400

Inclination Feature Label	Inclination (maxima or minima)	European Age (radiocarbon years BP)
α	Maximum	250(m)
β	Minimum	650(a)
γ	Maximum	1,250(a)
δ	Minimum	1,650(a)
ε	Maximum	3,000
ζ	Minimum	3,600
η	Maximum	3,750
ϑ	Minimum	4,500
ι	Maximum	5,200
κ	Minimum	6,100
λ	Maximum	7,300
μ	Minimum	8,400
ν	Maximum	9,700

(i) All ages are quoted in uncorrected radiocarbon years before present (Turner and Thompson, 1981; Creer and Tucholka, 1982a)

(ii) Data from the Magnetic Observatory, London, are designated with the suffix (m); declination feature A corresponds to data recorded in AD1815, while inclination feature α corresponds to data recorded in AD1715

(iii) Data from archaeomagnetic studies (Kovacheva, 1980) are designated with the suffix (a)

The measurement of the natural remanent magnetization of long sediment cores collected from Loch Morar, was therefore undertaken by the author with the purpose of attempting a correlation between the palaeomagnetic secular variation record from this site with the European type curves *sensu* Creer and Tucholka (1982a). Furthermore, the palaeomagnetic data were evaluated for the purpose of constructing an integrated chronological model for dating the sedimentary succession.

SOME TERMS AND DEFINITIONS USED IN THE STUDY OF PALAEOMAGNETISM

The Magnetization (M) or more precisely, the magnetic moment of a given substance may be regarded as comprising two components, namely remanent and induced magnetization:-

(i) Remanent magnetization arises when a substance is subjected to an applied magnetic field. After removal from the applied field the substance may retain a stable component termed remanent magnetization arising from the effect of the applied magnetic field.

(ii) Induced magnetization may also arise when the substance is subjected to an applied magnetic field. After removal from the applied field, however, the component of induced magnetization subsequently disappears from the substance.

In the case of rocks and unconsolidated sediments of geological origin, the total magnetization (M) comprises the vector sum of the remanent magnetization and the induced magnetization, arising from the influence of the Earth's magnetic field (McElhinny, 1973).

The magnetic susceptibility (κ) of a given substance can be broadly quantified as a ratio of magnetization (M) induced by an applied magnetic field strength (H), i.e. $\kappa = M/H$, where κ is strictly defined as a function of H, rather than as a constant of proportionality.

The ratio of the intensity of remanent magnetization (J) to magnetic susceptibility (κ) of rocks and sediments of geological origin is termed the Q-ratio, where $Q = J/\kappa$ (Koenigsberger, 1938).

The stability of remanent magnetization of a geological material is generally indicated where the Q-ratio is greater than 1.0. It is important to note that the term magnetic field strength (H) is often regarded in early literature as broadly equivalent to the term magnetic induction (B). Both terms are, however, distinct.

Thus, magnetic induction (B) pertains to a vacuum or air medium, while magnetic field strength (H) pertains to the solid state, where the magnetic permeability (μ) of the material substance is also implicated.

The relationship between the rationalized Systèm International d'Units (SI) established in 1948, and the centigrade, gramme, second (CGS) system of electromagnetic units for H, B and M respectively, is indicated in Table 29. Data from the palaeomagnetic analyses of the sediment cores from Loch Morar are expressed in CGS electromagnetic units.

SAMPLE PREPARATION AND MEASUREMENT OF THE NRM OF THE SEDIMENT CORES FROM LOCH MORAR

Palaeomagnetic analyses were carried out on cubic sediment samples removed with plastic boxes at 2.5 centimetres consecutive intervals down the sediment cores collected from Loch Morar; in most cases pairs of boxes were used at each sampling interval. The plastic boxes were marked *in situ* with the sampling interval depth and an azimuthal arrow indicating the top of the sediment core, i.e. in the vertical plane. The plastic boxes containing sediment were carefully cut from the core and affixed with lids and then sealed. The samples were stored in large air-tight plastic containers to minimize desiccation of the sediment samples. Core 1 from Loch Morar was sampled between 0 and 4.765 metres depth, with plastic boxes measuring 5.31 cubic centimetres, while Core 2 from Loch Morar was sampled between 0 and 4.825 metres depth, with plastic boxes measuring 5.70 cubic centimetres.

The natural remanent magnetization of the samples was measured at the Palaeomagnetic Laboratory, Department of Geophysics, University of Edinburgh, with a Digico balanced fluxgate spinner magnetometer (Creer *et al*, 1972), surrounded by a Faraday cage measuring *circa* 3 cubic metres, which accommodated one person operating the instrumentation. The initial magnetic susceptibility of the samples was measured separately by using a resistance bridge with a Digico air-cored solenoid. Individual samples were placed in the sample holder of the fluxgate magnetometer in a prescribed sequence of orthogonal orientations, referred to as the six-spin procedure, and rotated successively through 1800 revolutions at low speed per orientation, i.e. about three orthogonal axes. The spinner magnetometer can quantify the magnetization, or more precisely the magnetic moment of a sample, by virtue of the principle of electromagnetic induction (Faraday, 1832), whereby the rotation of a magnetic moment (in this case, pertaining to the sediment sample) within a coiled conductor induces an alternating electromotive force (emf), whose amplitude and

Table 29 - The relationship between SI and CGS electromagnetic units

Quantity	SI Unit (rationalized)	Equivalent CGS Unit (electromagnetic)
Magnetic Field Strength (H)	1 Ampere metre^{-1} (Am^{-1})	$4\pi \times 10^{-3}$ Oersted (Oe)
Magnetic Induction (B)	1 Tesla (T)	10^{4} gauss (G)
Magnetization (M)	1 Ampere metre^{-1} (Am^{-1})	10^{-3} Oersted (Oe)

Source: adapted from Tennent (1989)

phase can be detected and measured electronically. The magnetometer measures the component of magnetic moment which is orientated at right angles to the axis of rotation, thus the vectors of magnetization can be quantified by spinning the sample about three orthogonal axes. Generally, a procedure involving six spins is adopted for measuring samples (McElhinny, 1973). The intensity of magnetization per unit volume was also measured with the magnetometer. Thus, for Core 1, which yielded 326 samples, a total of 5,868 data were obtained by measuring the three components with a six-spin procedure, while for Core 2 which yielded 323 samples, a total of 5,814 data were obtained. The magnetometer was routinely checked after measuring between 5 to 10 samples, using a calibration specimen with an intensity of magnetization equal to 1.9344 x 10^4 μG/cm. A mean value of declination, inclination and intensity of magnetization for each sample was synchronously computed with an integrated microcomputer (MX1E) unit. The entire data were printed in digital form on paper, while the mean values were logged in an analogue form and subsequently processed with mainframe computer facilities at University of Edinburgh.

RESULTS OF THE ANALYSES OF THE NRM OF THE SEDIMENT CORES FROM LOCH MORAR

The palaeomagnetic data for the two sediment cores from Loch Morar are presented in Figures 13 to 16 as a series of graphical logs, which display the following magnetic parameters: remanent declination, remanent inclination, intensity of magnetization, magnetic susceptibility, and Q-ratio, plotted against depth down the respective sediment cores.

The magnetic parameters are quoted in unrationalized units from the CGS electromagnetic system of units, thus intensity of magnetization per unit volume is expressed in μG, initial magnetic susceptibility is expressed in μG/Oe, and Q-ratio is expressed in Oe.

The logs of intensity and susceptibility are plotted respectively as normal logarithmic values (i.e. Log_{10}) on the x-axis versus depth down the core on the y-axis.

Data for each core are presented both as the entire data set for the core plotted against depth in metres, and separately as the data set for the upper metre of the core plotted against depth in centimetres. The latter data set is also augmented with an abbreviated description of the lithostratigraphy of the sediment. The magnetic parameters are thus:-

(i) Declination (D) defined as the horizontal angle between the magnetic and geographical meridians. The geometrical features are labelled with capital Greek letters.

(ii) Inclination (I) defined as the vertical angle between the magnetic equator and the geographical latitude. The geometrical features are labelled with lower case Greek letters.

(iii) Intensity of magnetization (J) measured in μG per unit volume.

(iv) Magnetic susceptibility (κ) measured in μG/Oe.

(v) Q-ratio (J/κ) derived in Oe.

The intensity of magnetization (J) of the samples from the Loch Morar cores was measured (per unit volume) in air, consequently, the data are expressed in units of μG, i.e. magnetic induction. The magnetic susceptibility (κ) of the samples, however, represents the magnetic moment induced by a steady low field strength, consequently, these data are expressed in units of μG/Oe.

Files of data were recorded on magnetic tape and checked using a VAX mainframe computer system. The magnetic susceptibility of all the samples from the Morar cores was measured separately by using a resistance bridge with a Digico air-cored solenoid. The individual samples were subjected to a steady magnetic field strength, approximately equivalent to the ambient magnetic field strength of the Earth. The magnetic susceptibility apparatus measures in air the magnetic moment induced in a specimen which is subjected to a low steady field strength, measuring approximately 1 Oersted. The ratio of induced magnetization to applied magnetic field strength was automatically computed by an integrated microprocessor in the susceptibility unit. This computed ratio is termed the magnetic susceptibility (κ). Thus, Core 1 yielded 326 data, while Core 2 yielded 323 data. The mean magnetic susceptibility of the sample holder (i.e. κ_h) used to measure the samples from both cores was less than 1.0μG/Oe. Thus for Core 1 samples, $\kappa_h = 0.11 \pm 0.18$ μG/Oe, while for Core 2 samples $\kappa_h = 0.05 \pm 0.02$ μG/Oe. The magnetic susceptibility unit was routinely checked during sample measurement, using a calibration specimen with a specific magnetic susceptibility of 40.28μG/Oe. The magnetic susceptibility data for each core were merged with the relevant files of declination, inclination and intensity data stored on computer. A fifth parameter, termed the Q-ratio, was subsequently computed for all the samples, from the ratio of intensity of magnetization to magnetic susceptibility.

Fig.13 Logs of n.r.m. from Loch Morar sediment core 1 (0 to 5 m)

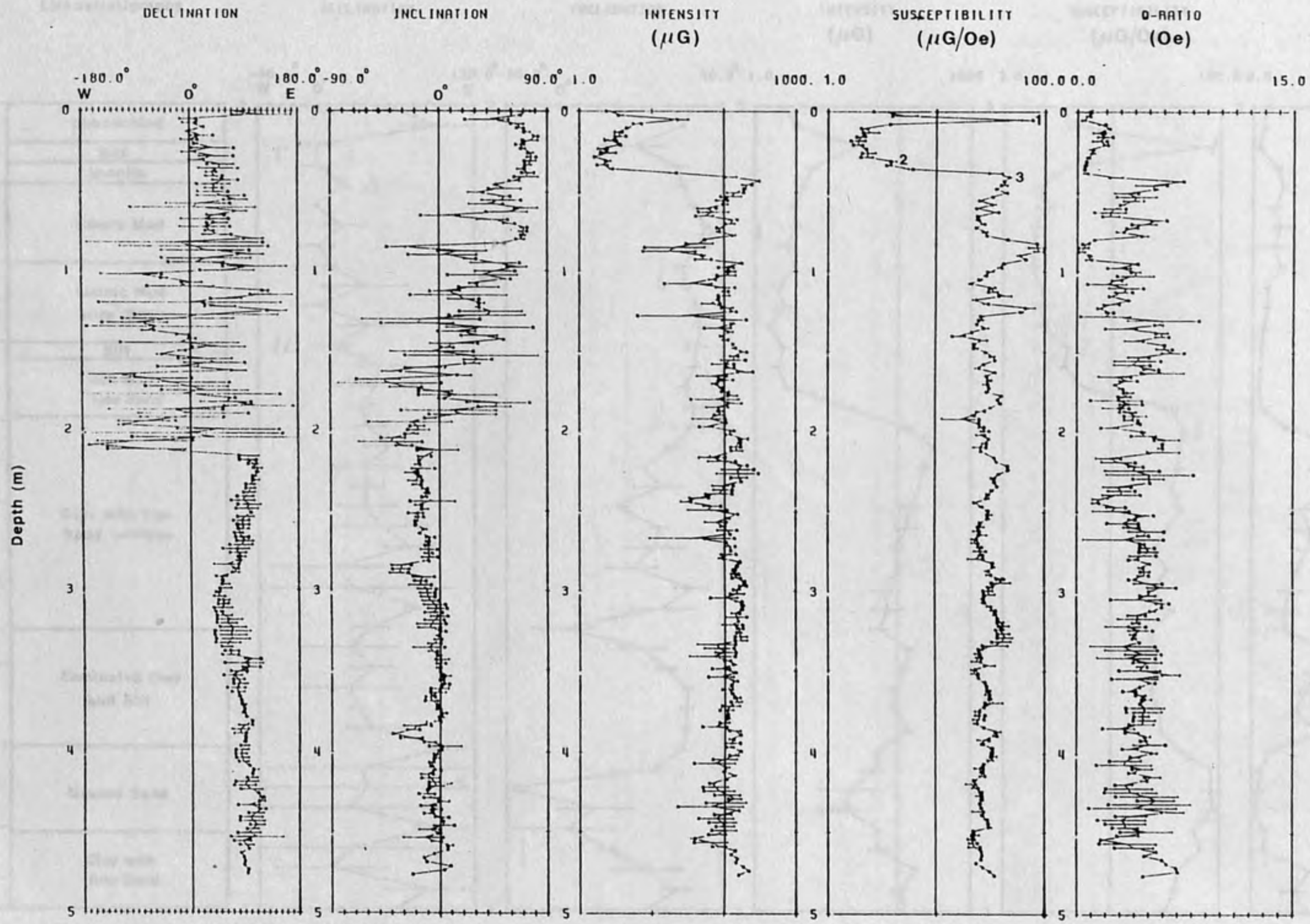


Fig.14 Logs of n.r.m. from Loch Morar sediment core 1 (0 to 100 cm)

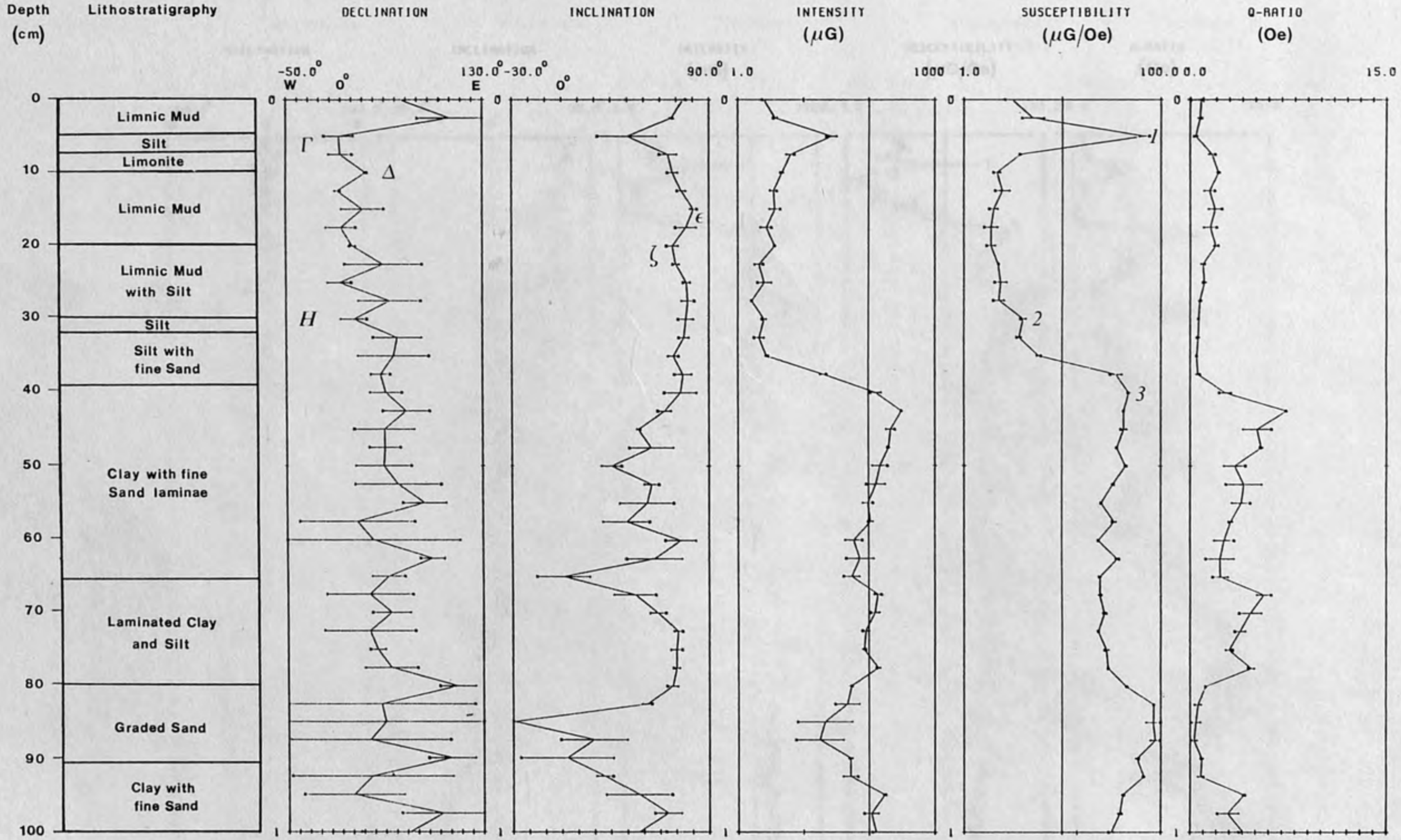


Fig.15 Logs of n.r.m. from Loch Morar sediment core 2 (0 to 5 m)

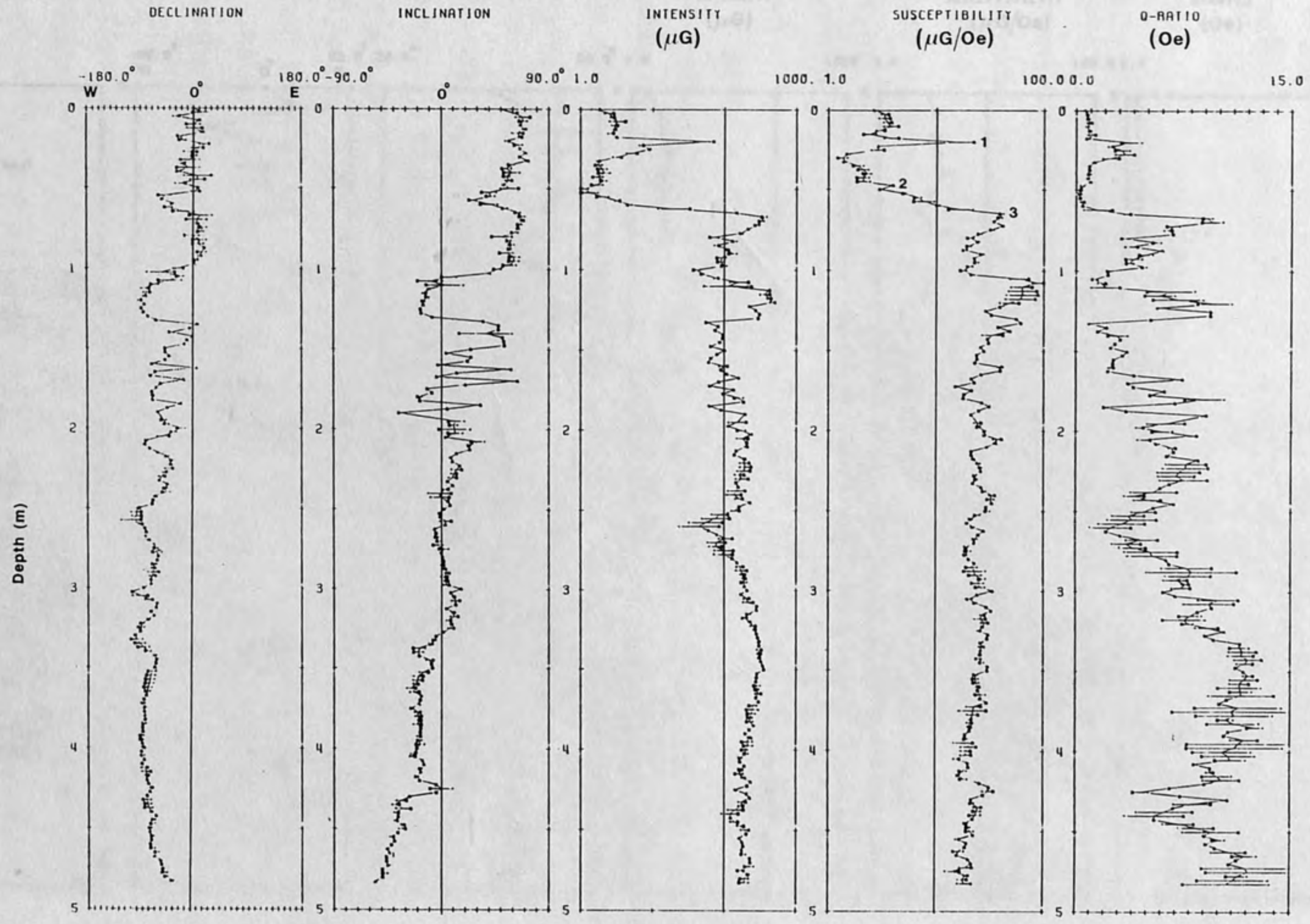
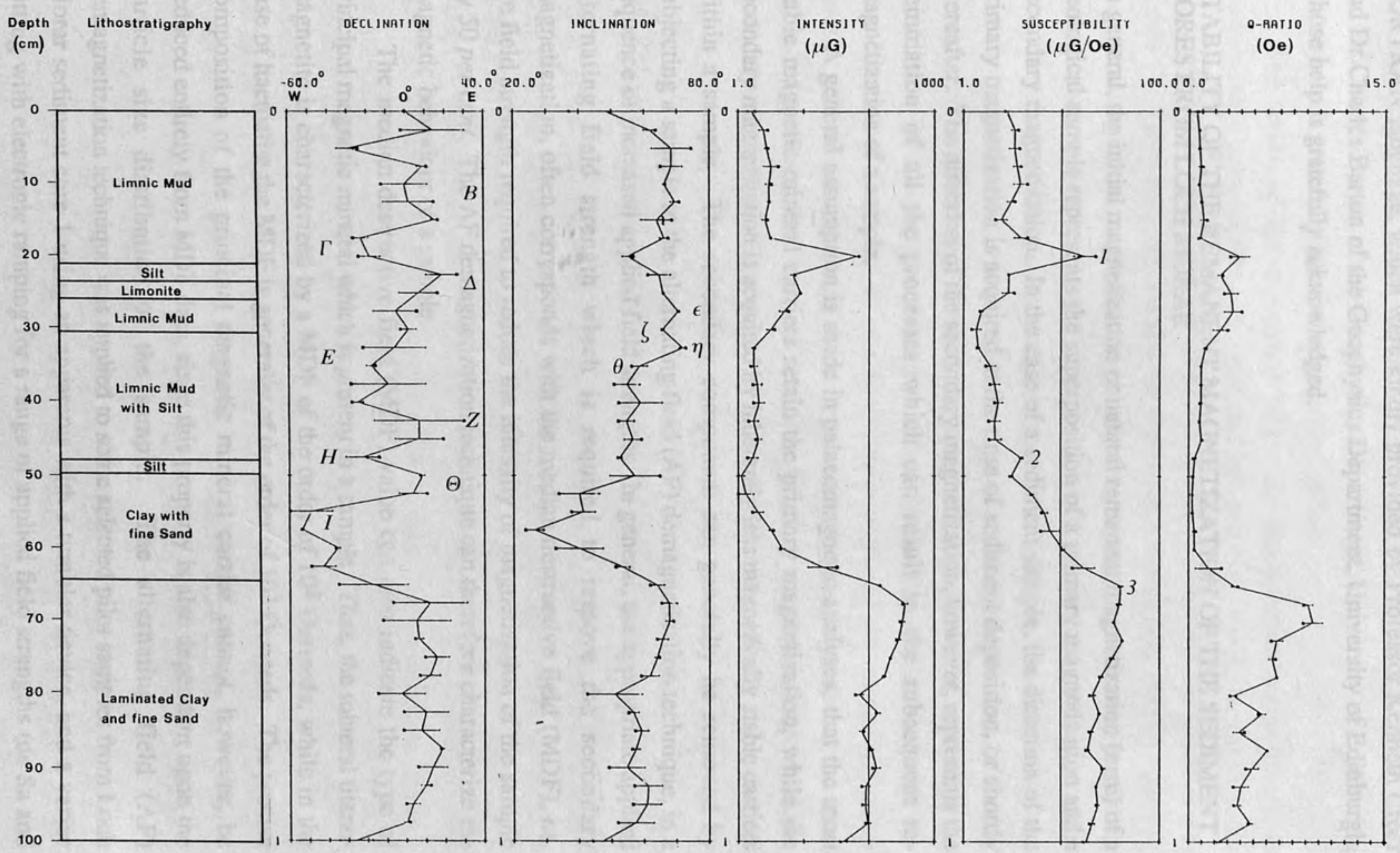


Fig.16 Logs of n.r.m. from Loch Morar sediment core 2 (0 to 100cm)



These Q-ratio data were merged with the relevant data files for each core. Thus, Core 1 yielded a further 326 data and Core 2 yielded a further 323 data. These data were processed using sophisticated computer programs compiled in FORTRAN language, which were kindly provided by Professor Kenneth Creer and Dr Charles Barton of the Geophysics Department, University of Edinburgh, whose help is gratefully acknowledged.

STABILITY OF THE REMANENT MAGNETIZATION OF THE SEDIMENT CORES FROM LOCH MORAR

In general, the initial magnetization or natural remanent magnetization (nrm) of a geological sample represents the superposition of a primary magnetization and a secondary magnetization. In the case of a sediment sample, the direction of the primary magnetization is acquired at the time of sediment deposition, or shortly thereafter. The direction of the secondary magnetization, however, represents the summation of all the processes which can result in the subsequent re-magnetization of a sample.

A general assumption is made in palaeomagnetic analyses, that the most stable magnetic mineral carriers retain the primary magnetization, while the secondary magnetization is acquired by inherently less magnetically stable carriers within a sample. The secondary component can generally be removed by subjecting a sample to the alternating field (AF) demagnetization technique, in a sequence of increased applied field strengths. In general, the appropriate applied alternating field strength which is required to remove the secondary magnetization, often corresponds with the median destructive field (MDF), i.e. the field strength required to reduce the intensity of magnetization of the sample by 50 *per cent.* The AF demagnetization technique can therefore characterize the magnetic behaviour of a sample.

The median destructive field (MDF) value can also indicate the type of principal magnetic mineral which is present in a sample. Thus, the mineral titano-magnetite is characterized by a MDF of the order of 10^2 Oersteds, while in the case of haematite the MDF is generally of the order of 10^3 Oersteds. The precise composition of the principal magnetic mineral carrier cannot, however, be deduced entirely from MDF data, since this property is also dependent upon the particle size distribution of the sample. The alternating field (AF) demagnetization technique was applied to some selected pilot samples from Loch Morar sediment core 1 using an apparatus with a tumbler device, and a variac setting with electronic ramping for a range of applied field strengths (de Sa and Widdowson, 1975). The pilot samples were selected from the limnic mud and silt, and clay sediments represented in the lithostratigraphic succession of the sediment cores. The samples were subjected to a series of progressively increasing applied demagnetizing field strengths at 400 Hertz frequency, along three orthogonal axes, up to a peak field strength of 900 Oersteds. The nrm of the individual samples were remeasured with a Digico magnetometer following each application of an alternating demagnetizing field.

The results of the application of the AF demagnetization technique to representative samples of limnic mud and silt, and clay, are presented in Table 30. Two AF demagnetization curves derived from these data are illustrated in Figure 17. These data indicate that the median destructive field (MDF) values of the pilot samples are within the range of *circa* 250-300 Oe, which suggests that titano-magnetite is the principal magnetic mineral carrier in the sediment cores from Loch Morar. The presence of titanomagnetite in the sediments is consistent with the character of the mineral detritus originating from the Moine schist rock, and Lewisian gneiss inliers of the Morar Basin.

These data also reveal that the remanent declination and inclination of the pilot samples generally remain stable within an applied field strength up to the median destructive field and show no systematic change in the remanence, indicating that the nrm of the sediment cores from Loch Morar probably reflect a predominantly stable primary magnetization.

THE PALAEOMAGNETIC SECULAR VARIATION RECORD FROM LOCH MORAR

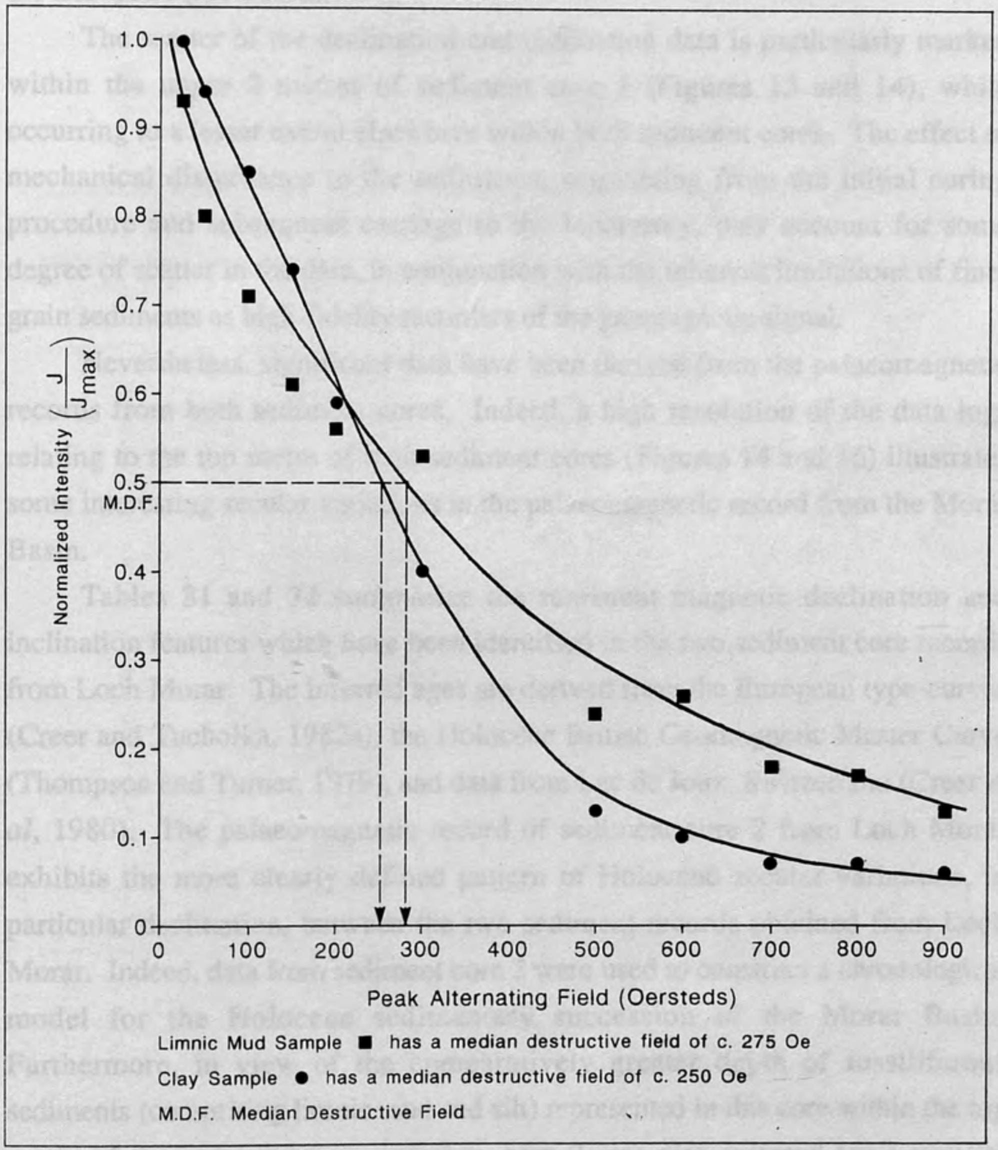
The graphical logs illustrating the secular variation in declination for the Morar Basin (Figures 12-16) have been centred around the mean declination value (D_m) of the axial dipole field, namely 0°, as described previously in the context of the European type-curves *sensu* Creer and Tucholka (1982a). The inclination data have been plotted without being centred around a mean inclination value. Indeed, the orientation of laminations in the lithostratigraphic record exhibited by both sediment cores indicated that the Mackereth corer had penetrated the sedimentary succession in an approximately perpendicular plane. Consequently, no correction was applied to the inclination data. The inclination value of the axial geocentric dipole field *sensu* McElhinny (1973) for the Morar Basin (Latitude 56°58') is computed to be 74° positive; inclination data for the uppermost sediments in both cores generally approximate to this value.

The palaeomagnetic record from both sediment cores proved easiest to interpret where the lithostratigraphic succession comprised limnic mud and silt. Indeed, these sediments were best represented, in terms of depth of sediment accumulation, in sediment core 2. The palaeomagnetic record proved difficult to

Table 30 - Typical AF demagnetization data for sediment samples from Loch Morar sediment core 1

Sediment sample description	*Peak alternating demagnetizing field (Oersteds)*							
	0	25	50	100	150	200	300	500
(i) Limnic mud from 5.0cm; [*] in Figure 17								
Normalized intensity	1.00	0.933	0.800	0.708	0.612	0.565	0.530	0.243
Declination	199.1	193.2	194.3	190.1	191.1	190.3	191.5	184.8
Inclination	32.5	35.5	32.3	33.3	39.6	38.4	35.4	32.8
(ii) Limnic mud with silt from 22.5cm								
Normalized intensity	1.00	0.758	1.070	0.961	0.815	0.705	0.586	0.246
Declination	245.6	239.2	236.8	213.7	215.0	254.3	199.5	189.0
Inclination	68.6	68.1	72.2	66.8	68.6	74.8	46.6	20.4
(iii) Clay with fine sand from 122.5cm								
Normalized intensity	1.00	1.021	0.954	0.872	0.754	0.616	0.441	0.130
Declination	238.4	237.7	234.8	232.7	299.1	229.1	225.1	227.7
Inclination	30.3	29.6	28.6	27.0	26.9	25.7	26.5	28.7
(iv) Clay from 187.5cm; [•] in Figure 17								
Normalized intensity	1.00	0.998	0.944	0.854	0.736	0.591	0.400	0.127
Declination	264.9	265.6	263.3	262.8	258.4	256.8	254.0	254.1
Inclination	-32.0	-32.5	-33.6	-36.0	-35.8	-38.7	-39.2	-39.5

Fig.17 ALTERNATING FIELD DEMAGNETIZATION DATA FOR TWO SAMPLES FROM LOCH MORAR SEDIMENT CORE 1



interpret where the lithostratigraphic succession comprised clay and sand. The change in lithostratigraphy from limnic mud and silts to clay and sand occurred within the top metre of both sediment cores.

The palaeomagnetic record from sediment core 2 (Figures 15 and 16) exhibits several features of declination and inclination variations within the top metre of sediment, which can be correlated with the European type-curves *sensu* Creer and Tucholka (1982a). The palaeomagnetic record from sediment core 1 however, is rather less clearly defined. Consequently, only a few features of declination and inclination variation were tentatively assigned and correlated with the European type-curves.

The scatter of the declination and inclination data is particularly marked within the upper 2 metres of sediment core 1 (Figures 13 and 14), while occurring to a lesser extent elsewhere within both sediment cores. The effect of mechanical disturbance to the sediments, originating from the initial coring procedure and subsequent carriage to the laboratory, may account for some degree of scatter in the data, in conjunction with the inherent limitations of fine-grain sediments as high-fidelity recorders of the geomagnetic signal.

Nevertheless, significant data have been derived from the palaeomagnetic records from both sediment cores. Indeed, a high resolution of the data logs relating to the top metre of both sediment cores (Figures 14 and 16) illustrates some interesting secular variations in the palaeomagnetic record from the Morar Basin.

Tables 31 and 32 summarize the remanent magnetic declination and inclination features which have been identified in the two sediment core records from Loch Morar. The inferred ages are derived from the European type-curves (Creer and Tucholka, 1982a), the Holocene British Geomagnetic Master Curve (Thompson and Turner, 1979), and data from Lac de Joux, Switzerland (Creer *et al*, 1980). The palaeomagnetic record of sediment core 2 from Loch Morar exhibits the more clearly defined pattern of Holocene secular variations, in particular declination, between the two sediment records obtained from Loch Morar. Indeed, data from sediment core 2 were used to construct a chronological model for the Holocene sedimentary succession of the Morar Basin. Furthermore, in view of the comparatively greater depth of fossiliferous sediments (comprising limnic mud and silt) represented in this core within the top metre of the sedimentary succession, core 2 was also selected for a parallel investigation of the micro-fossil record. The results of this investigation are reported later in this chapter.

Table 31 - Remanent magnetic declination and inclination features identified in nrm data from Loch Morar sediment core 1

Declination Feature Label	Declination (θ_W or θ_E)	Depth in Core (cm)	European Age (radiocarbon years BP)
A	Westerly		150
B	Easterly		1,200
Γ	Westerly	5.0-7.5	2,000
Δ	Easterly	10.0-12.5	2,500
E	Westerly		4,200
Z	Easterly		6,300
H	Westerly	30.0-32.5	7,400

Inclination Feature Label	Inclination (maxima or minima)	Depth in Core (cm)	European Age (radiocarbon years BP)
α	Maximum		250
β	Minimum		650
γ	Maximum		1,250
δ	Minimum		1,650
ε	Maximum	15.0-17.5	3,000
ζ	Minimum	20.0-22.5	3,600
η	Maximum		3,750
ϑ	Minimum		4,500
ι	Maximum		5,200
κ	Minimum		6,100
λ	Maximum		7,300
μ	Minimum		8,400
ν	Maximum		9,700

Table 32 - Remanent magnetic declination and inclination features identified in the nrm data from Loch Morar sediment core 2

Declination Feature Label	Declination (θ_W or θ_E)	Depth in Core (cm)	European Age (radiocarbon years BP)
A	Westerly		150
B	Easterly	7.5-17.5	1,200
Γ	Westerly	17.5-2.5	2,000
Δ	Easterly	22.5-25.0	2,500
E	Westerly	32.5-35.0	4,200
Z	Easterly	42.5-45.0	6,300
H	Westerly	47.5-50.0	7,400
Θ	Easterly	50.0-52.5	8,800
I	Westerly	55.0-57.5	9,900

Inclination Feature Label	Inclination (maxima or minima)	Depth in Core (cm)	European Age (radiocarbon years BP)
α	Maximum		250
b	Minimum		650
g	Maximum		1,250
δ	Minimum		1,650
ε	Maximum	27.5-30.0	3,000
ζ	Minimum	30.0-32.5	3,600
η	Maximum	32.5-35.0	3,750
ϑ	Minimum	35.0-37.5	4,500
ι	Maximum		5,200
k	Minimum		6,100
λ	Maximum		7,300
μ	Minimum		8,400
ν	Maximum		9,700

The discussion of the palaeomagnetic record from Loch Morar consequently focuses upon data from sediment core 2, while drawing appropriate parallels with data from sediment core 1.

The principal features of the secular variation recorded in the Morar sediment cores are labelled with capital Greek letters for the declination data, and lower case Greek letters for the inclination data, respectively. The horizontal scale divisions in the logs denote increments of ten degrees, while the vertical scale divisions denote increments of depth down the respective sediment cores.

A direct comparison between the record from Loch Morar and the European type-curves (*sensu* Creer and Tucholka, 1982a) is illustrated in Figure 18. The amplitude of the declination variations recorded in the upper 50 centimetres of Loch Morar sediment core 2, range between *circa* ±30°, while the inclination variations range between *circa* 50° and 75° positive.

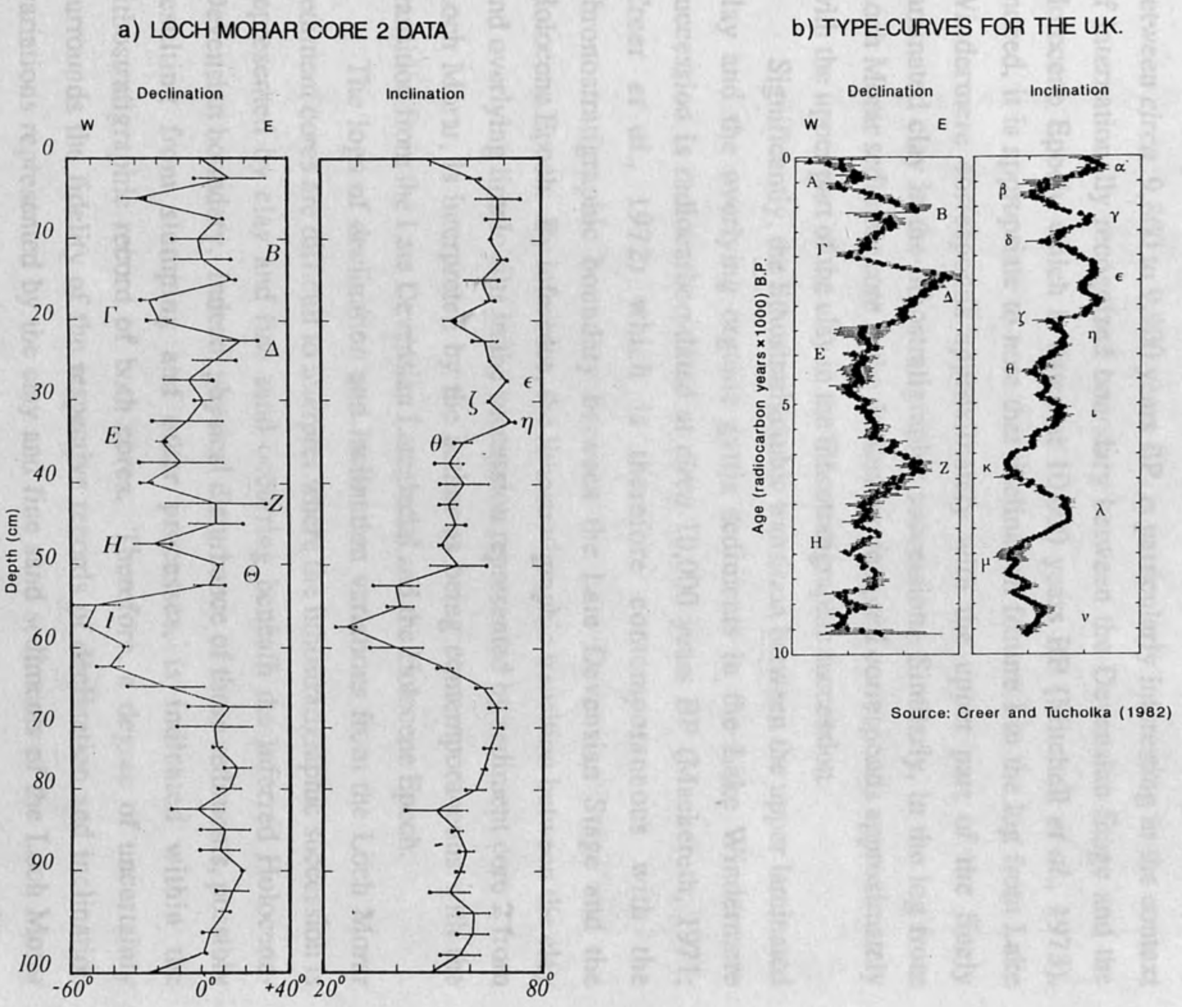
The general agreement between the data illustrated in Figure 18, and the correspondence of the inclination data from Loch Morar with the expected inclination value of 74.0° positive (computed for a time-averaged geocentric axial dipole field during the Holocene Epoch) suggests that the uppermost sediments in both cores from Loch Morar are the products of deposition during the Holocene Epoch. A corresponding examination of fossil tree pollen from sediments ranging from the top of core 2, i.e. zero datum to 60 centimetres depth, reported later in this chapter, confirmed this view. Furthermore, the fossil pollen record also provided an independent dating control for the declination features exhibited in the palaeomagnetic record from core 2.

Two additional declination features have been assigned to the declination record from Loch Morar, which are not designated in the European type-curves (Creer and Tucholka, 1982a). These two features are labelled as Θ (theta) and I (iota), respectively, in the graphical logs for Loch Morar data; they precede the westerly feature H (eta), with Θ (theta) denoting an easterly feature, and I (iota) denoting a westerly feature respectively.

Although these two features are not designated in the European type-curves (Creer and Tucholka, 1982a), they are nevertheless, discernible in records from various sites in western Europe, including Lake Windermere, UK (Creer *et al*, 1976), Lac de Joux, Switzerland (Creer *et al*, 1980), Torreberga, Sweden (Sandgren, 1986) and Llyn Gwernan, UK (Austin and Lowe, 1989).

The westerly declination feature corresponding to Θ (theta) is dated in the European records within the range *circa* 8,250-8,800 years BP. This feature is dated at 8,800 years BP in the Holocene British Geomagnetic Master Curve (HBGMC) *sensu* Thompson and Turner (1979). The easterly declination feature corresponding to I (iota) is dated in the European records within the range *circa*

Fig.18 LOCH MORAR DATA COMPARED WITH THE TYPE CURVES FOR THE U.K.



a) LOCH MORAR CORE 2 DATA

b) TYPE-CURVES FOR THE U.K.

Source: Creer and Tucholka (1982)

9,800-9,900 years BP. This feature is dated at 9,900 years BP in the HBGMC *sensu* Thompson and Turner (1979).

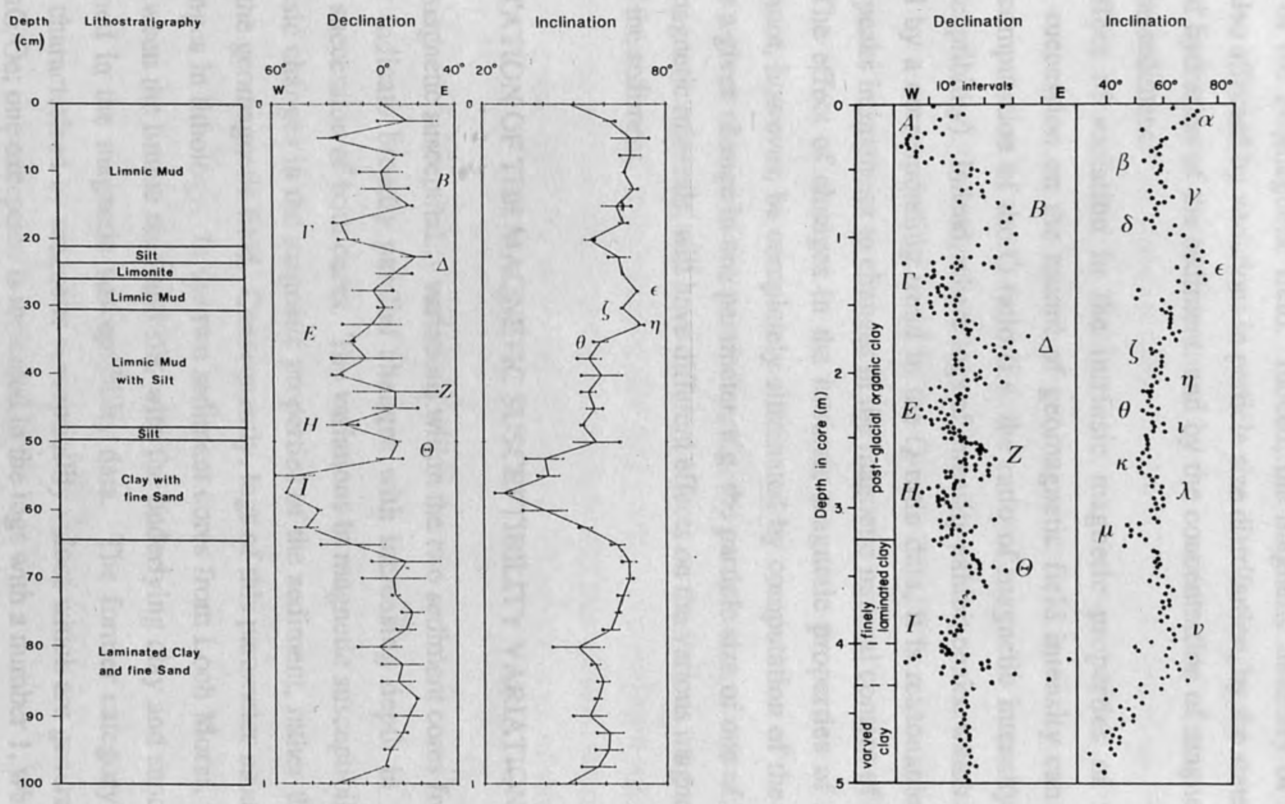
A comparison between the secular variation curves of relative declination and inclination recorded in sediment core 2 from Loch Morar, with composite curves from Lake Windermere (Creer *et al*, 1976) is illustrated in Figure 19. The logs of declination data exhibit a particularly strong correlation. Furthermore, the declination features Θ (theta) and I (iota) are clearly recognizable in the logs from both Loch Morar and Lake Windermere.

The declination feature I, which is dated from various European records at between *circa* 9,800 to 9,900 years BP, is particularly interesting in the context of internationally recognized boundary between the Devensian Stage and the Holocene Epoch, which is dated at 10,000 years BP (Mitchell *et al.*, 1973). Indeed, it is appropriate to note that declination feature I in the log from Lake Windermere corresponds approximately with the upper part of the finely laminated clay in the lithostratigraphic succession. Similarly, in the log from Loch Morar sediment core 2, the declination feature I corresponds approximately with the upper part of the clay in the lithostratigraphic succession.

Significantly, the lithostratigraphic transition between the upper laminated clay and the overlying organic gyttja sediments in the Lake Windermere succession is radiocarbon-dated at *circa* 10,000 years BP (Mackereth, 1971; Creer *et al.*, 1972) which is therefore contemporaneous with the chronostratigraphic boundary between the Late Devensian Stage and the Holocene Epoch. By inference, the lithostratigraphic transition between the clay and overlying limnic silts in the succession represented by sediment core 2 from Loch Morar, is interpreted by the author as being contemporaneous with the transition from the Late Devensian Lateglacial and the Holocene Epoch.

The logs of declination and inclination variations from the Loch Morar sediment cores are difficult to interpret where the lithostratigraphic succession is represented by clay and fine sand occurring beneath the inferred Holocene-Devensian boundary. Indeed, physical disturbance of these sediments, possibly resulting from slumping and other processes, is indicated within the lithostratigraphic record of both cores. Therefore, a degree of uncertainty surrounds the fidelity of the respective records of declination and inclination variations represented by the clay and fine sand sediments of the Loch Morar cores.

Fig.19 LOCH MORAR DATA COMPARED WITH THE LAKE WINDERMERE COMPOSITE DATA



a) LOCH MORAR CORE 2 DATA

b) LAKE WINDERMERE COMPOSITE DATA

Source: Creer et al. (1976)

INTERPRETATION OF THE MAGNETIC INTENSITY VARIATIONS AND THE Q-RATIO

The logs of magnetic intensity variations within the two sediment cores from Loch Morar exhibit broadly parallel changes with increasing depth in the sediment succession of both cores. The interpretation of the variations in intensity data are complicated, however, for the variations are not solely determined by changes in the strength of the geomagnetic field. Indeed, the magnetic intensity of the sediment is also affected by variations in particle size distribution, by the state of oxidation and hydration of the sediment, and by the concentration of magnetic minerals in the sediment.

The effect of variation in the intrinsic magnetic properties of the sedimentary succession on the record of geomagnetic field intensity can be reduced by computation of the Q-ratio (i.e. the ratio of magnetic intensity to magnetic susceptibility). Indeed, where logs of intensity exhibit peaks, which are not reflected by a corresponding trend in the Q-ratio data, it is reasonable to attribute the peaks in intensity to changes in the magnetic mineral content of the sediment. The effect of changes in the intrinsic magnetic properties of the sediment cannot, however, be completely eliminated by computation of the Q-ratio because a given change in one parameter, e.g. the particle size of one of the constituent magnetic minerals, will have different effects on the various magnetic properties of the sediment.

INTERPRETATION OF THE MAGNETIC SUSCEPTIBILITY VARIATIONS

The logs of magnetic susceptibility variations within the two sediment cores from Loch Morar indicate broadly parallel changes with increasing depth in the sedimentary succession of both cores. The variations in magnetic susceptibility reflect intrinsic changes in the magnetic properties of the sediment, rather than variation in the geomagnetic field. Consequently, logs of this parameter usually indicate changes in lithology. In the two sediment cores from Loch Morar, the interface between the limnic mud and silt, with the underlying clay and sand is clearly defined in the magnetic susceptibility data. The former category of sediments is characterized by magnetic susceptibility values which are generally less than 10µG/Oe; one exception is indicated in the logs with a number 1, which corresponds to a thin layer of silt, which was preserved in both sediment cores. The clay and sand which underlie the limnic mud and sils are characterized by magnetic susceptibility values which are generally greater than 10µG/Oe and range between 10 to 100 µG/Oe. The sediments which represent the lithological transition between the limnic mud and silt, sediments and clay and sand proper are characterized by magnetic susceptibility values which are intermediate within the overall range of data. This transition is indicated in the logs for both cores with the numbers 2 and 3, respectively. Broadly similar variations in the magnetic susceptibility data from both sediment cores also correlate with parallel changes in the lithostratigraphic succession indicated in Tables 24 and 25.

A direct indication of erosion, and in turn soil degradation, within the drainage area of the basin is also provided by the record of magnetic susceptibility variations in sediment cores. Indeed, where there is a relative increase in the rate of erosion within the catchment area of a basin, the removal of magnetic minerals from bedrock or unconsolidated deposits usually increases in relative terms. The eroded detrital material is subsequently transported by water into the basin, where it becomes incorporated within the sedimentary succession. Therefore, peaks of magnetic susceptibility within a log of magnetic susceptibility variations, generally reflect episodes of relatively increased erosion of the magnetic minerals within the catchment area of the basin (Thompson *et al*, 1975). The logs of magnetic susceptibility and magnetic intensity variations exhibited by the two sediment cores from Loch Morar indicate that a marked change in the values of both parameters occured, in particular, between the lower limit of the limnic mud and silt, and the upper limit of the laminated clay and fine sand in the sedimentary succession.

This change may be attributed to an alteration in the sediment input regime occurring within the catchment area of the basin, i.e. from a regime dominated by conditions of mass input to selective input via channels and streams. Significantly, data from the log of magnetic declination for sediment core 2 indicate that this marked change correlates with the lower boundary of the Holocene Epoch dated at 10,000 years BP. Therefore, the underlying laminated clays probably represent sub-glacial or pro-glacial sediments which were deposited during the Loch Lomond Stadial (i.e. between *circa* 11,000 to 10,000 years BP). Indeed, the postulated limit of the Loch Lomond Stadial ice apparently extended westward across the Morar Basin, with an ice margin situated along the present western shore of Loch Morar (Peacock, 1970). The glacier ice associated with the Loch Lomond Stadial is considered to have extended from the high eastern mountains near the present principal watershed, in a westward direction across the region which is now occupied by Loch Morar; lithostratigraphic evidence from an adjacent hill lochan called Lochan a'Chleirich, presented earlier in this chapter, supports the postulated western limit of the ice occurring in the vicinity of the western shore of Loch Morar. The two sediment cores from Loch Morar were collected from two locations situated in the western region of the loch, at a distance of between *circa* 1.62 kilometres and 1.41

kilometres respectively, from the western shore and hence within the postulated limit of the Loch Lomond Stadial ice margin.

Increased relative erosion rates and soil degradation arising from the impact of forest clearances and intensive indigenous agricultural practices during the Holocene Epoch, have been elucidated using magnetic susceptibility profiles in conjunction with fossil data from lacustrine sites in different geographical regions, including Lough Neagh, Northern Ireland (Thompson *et al.*, 1975), Loch Lomond (Dickson *et al.*, 1978) and Braerodach Loch, Scotland (Edwards and Rowntree, 1980), various Scandinavian lakes (Thompson *et al.*, 1980) and Lake Egari, Papua New Guinea (Oldfield *et al.*, 1985). Furthermore, relative changes in the contribution of mineral detritus originating from different sources, e.g. bedrock *versus* top soil, have also been determined using magnetic susceptibility profiles of sediment cores collected from Chesapeake Bay, eastern United States (Thompson and Oldfield, 1986).

Changing magnetic susceptibility in the sediment profiles appears to be positively correlated with variations in the input of inwashed allocthonous detritus at these sites.

The pattern of magnetic susceptibility variations post-10,000 years BP recorded in the sediment cores from Loch Morar, is interpreted as possibly resulting from processes associated with maturation of soils and vegetation, with minimal anthropogenic influence within the catchment area of the Morar Basin, as described in the Cumbrian Lake District, England by Mackereth (1966), coupled with a declining allocthonous contribution to the lacustrine sediments, until at least *circa* 3,600 years BP to 3,000 years BP. After this date the magnetic susceptibility began to rise perhaps as a result of anthropogenic activities, including localized forest clearance and settlement.

THE FOSSIL POLLEN RECORD FROM THE LOCH MORAR SEDIMENTARY SUCCESSION

INTRODUCTION

The application of non-destructive techniques to measure the natural remanent magnetism of the sediment cores from Loch Morar enabled the author to undertake a subsequent analysis of the microscopic fossil record preserved in the sedimentary succession. The palaeomagnetic secular variation record from sediment core 2 provided a chronological framework for interpreting temporal changes in the fossil record. Furthermore, the possibility also existed whereby the fossil pollen record from Loch Morar could be correlated with published fossil data from other locations also situated with the zone of potential oak with birch woodland cover (*sensu* McVean and Ratcliffe, 1962), thus providing independent chronological markers for the palaeomagnetic record, and additional information about the history of the native woodland cover of the Morar Basin.

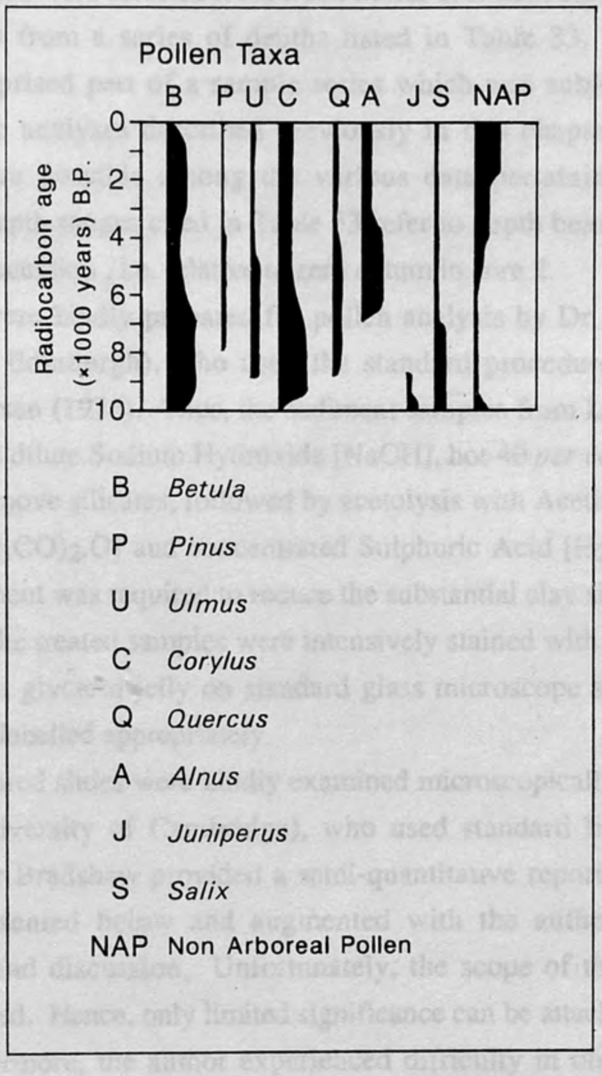
Fossil pollen data from locations within the area of potential oak with birch woodland cover (*sensu* McVean and Ratcliffe, 1962), independently reviewed by Birks, H.J.B. (1977) and Walker (1984) indicate that following the decay of glacier ice associated with the Loch Lomond Stadial/Younger Dryas Period, the emergent landscape of exposed bedrock and comminuted rock debris was initially colonized by pioneer plant communities, typically comprising lichens and herbaceous plants associated with tundra conditions. In response to continuing climatic amelioration, the shrub *Juniperus communis* became widely established at around 10,000 years BP. The presence of this taxon is indicative of a rapid increase in mean ambient summer temperature, which is reflected in an increased flowering of this shrub (Iversen, 1954). This was followed by the development of open deciduous woodland, initially comprising the tree birches, *Betula pubescens* and *B. verrucosa*, at *circa* 9,700 years BP, and later including *Corylus avellana*, which migrated along the western Scottish sea-board reaching Wester Ross by *circa* 8,800 years BP. The open birch and hazel woodlands also contained *Populus tremula, Sorbus aucuparia, Salix* species and *Prunus padus*. Although stands of *Juniperus communis* persisted in the landscape, they ceased to form a component of the birchwoods following the arrival of *Corylus avellana*.

The fossil pollen record indicates that the birch and hazel woodlands were invaded by *Quercus* (perhaps *Q. petraea*) and *Ulmus* (probably *U. glabra*) at *circa* 8,500 years BP to form mixed deciduous forest which contained *Ilex aquifolium, Sorbus aucuparia, Viburnum opulus, Hedera helix* and *Lonicera periclymenum*. Pteridophyte ferns were also common, from evidence of fossil spores, and these included the filmy fern *Hymenophyllum wilsonii*, indicating the oceanicity of the prevailing climate. *Fraxinus excelsior* was rare, and perhaps restricted to damp, mildly basic openings in the tree cover. *Tilia cordata* appears to have been absent from this region. *Pinus sylvestris* arrived at *circa* 8,000 years BP but evidently remained rare, occupying marginal habitats including raised bog surfaces, e.g. in Galloway, where it grew between *circa* 7,500 and 6,800 years BP, and where the tree stumps were subsequently buried by peat growth (Birks, H.H., 1975). Competition from deciduous trees including *Quercus* and *Ulmus*, and *Corylus avellana* may have restricted the availability of habitats for *Pinus sylvestris* early in the Holocene Epoch.

Between *circa* 7,500 and 4,000 years BP *Pinus sylvestris* cover increased, presumably forming forest communities on poorer soils and at higher altitudes than the broad-leaved deciduous forests. Indeed, during this period *Pinus sylvestris* attained its most extensive geographical distribution in the British Isles during the Holocene Epoch (Bennett, 1984). In Scotland, this tree species is estimated to have ranged over 800,000 hectares in extent during this period. However, *Pinus sylvestris* appears to have been either rare or absent from the extreme west and southwestern headlands during the Holocene Epoch. A fossil pollen record from Lochan Doilead, (National Grid reference: NM 676 946) situated *circa* 1.7 kilometres north of Morar, which is illustrated in Figure 20, indicates that *Pinus sylvestris* pollen did not exceed 20 *per cent* of the total arboreal pollen sum during this period, therefore suggesting that this taxon was probably a rare component in the native tree cover of this area (Williams, 1977; Birks, H.J.B., 1977). Between *circa* 6,500 and 6,250 years BP *Alnus glutinosa* expanded in wet habitats, where it largely replaced *Salix* species. In southeastern Skye and western Inverness-shire this taxon became an important local component in the tree cover during this period (Williams, 1977; Birks, H.J.B., 1977).Significantly, expanding populations of *Alnus glutinosa* also replaced some of the *Pinus sylvestris* communities in the British Isles, notably at waterlogged sites, during this period (Bennett, 1984). *Pinus sylvestris* pollen values in a record from Loch Maree, Wester Ross (Birks, H.H., 1972a), indicate a slow decline at *circa* 7,000 years BP, perhaps as a result of soil deterioration in the prevailing oceanic climate. This decline continued until *circa* 4,000 years BP (Birks, H.H., 1972a). Indeed, by *circa* 4,000 years BP *Pinus sylvestris* had become extremely restricted over much of its geographical range within the British Isles, eventually becoming confined to northern regions, mountainous areas and marginal habitats, including raised bogs, and the limestone plateaux of the Burren, western Ireland (Bennett, 1984). The reasons for the widespread and spectacular decline of Scots pine in northwest Scotland are not clear. However, it has been suggested that a combination of climatic changes and anthropogenic activity, including burning, may have initiated the replacement of Scots pine forest on flat and gently sloping ground by blanket bog (Birks, H.H., 1972a). Fossil tree stumps of *Pinus sylvestris* buried in blanket peat are widely reported from a number of localities, including the western sea-board of the Morar Basin (Figure 1 in Birks, H.H., 1975; Figure 2 in Bennett, 1984).

The indigenous woodland cover of the Highland Region also incurred extensive reduction, particularly during the last 2,000 years. Indeed, many areas the woodland cover have been replaced by *Sphagnum* bog, dwarf-shrub heath and acidic grassland communities. This trend is also indicated in the fossil record by relative increases in spores of *Sphagnum* species, and pollen of *Corylus avellana, Myrica gale, Calluna vulgaris*, Cyperaceae and Gramineae. The

Fig.20 RELATIVE PROPORTIONS OF HOLOCENE POLLEN TAXA FROM LOCHAN DOILEAD, WEST INVERNESS-SHIRE



Source: Birks, H.J.B. (1977)

remanent native woodland cover in the Morar Basin now predominantly comprises *Quercus* ref. *petraea, Betula pubescens* and *Corylus avellana,* with *Alnus glutinosa* and *Salix* species occurring on relatively wetter soils.

ANALYSIS OF THE FOSSIL POLLEN RECORD FROM THE LOCH MORAR SEDIMENTARY SUCCESSION

SAMPLE PREPARATION AND POLLEN ANALYSIS

Sediment samples were selected from Loch Morar sediment core 2 for fossil tree pollen analysis from a series of depths listed in Table 33. These samples originally comprised part of a sample series which was subjected to various palaeomagnetic analyses described previously in this chapter. Thus, direct comparisons are possible among the various data pertaining to a specific sample. The depth ranges cited in Table 33 refer to depth below the top of the sedimentary succession , i.e. relative to zero datum in core 2.

The samples were kindly prepared for pollen analysis by Dr Alan Alexander (University of Edinburgh), who used the standard procedures described by Faegri and Iversen (1975). Thus, the sediment samples from Loch Morar were treated with hot dilute Sodium Hydroxide [NaOH], hot 40 *per cent* Hydrofluoric acid [HF] to remove silicates, followed by acetolysis with Acetic Anhydride/Di-ethanone [$(CH_3CO)_2.O$] and concentrated Sulphuric Acid [H_2SO_4]; vigorous chemical treatment was required to reduce the substantial clay silicate content of the samples. The treated samples were intensively stained with purple saffranin and mounted in glycerol jelly on standard glass microscope slides with glass coverslips, and labelled appropriately.

The prepared slides were kindly examined microscopically by Dr Richard Bradshaw (University of Cambridge), who used standard light microscope equipment. Dr Bradshaw provided a semi-quantitative report of the findings which are presented below and augmented with the author's description, interpretation and discussion. Unfortunately, the scope of this analysis was extremely limited. Hence, only limited significance can be attached to these data *per se.* Furthermore, the author experienced difficulty in obtaining detailed information in connection with this analysis.

POLLEN DETERMINATIONS

The samples from the upper part of the sedimentary succession of core 2 yielded a relatively higher concentration of fossil pollen grains, compared with samples from the lower part of the succession. The state of preservation of the fossil

Table 33 - Sediment sample depths selected in Loch Morar sediment core 2 for fossil pollen analysis

Sample depth range (cm)
0.0-2.5
5.0-7.5
10.0-12.5
17.5-20.0
20.0-22.0
27.5-30.0
32.5-35.0
37.5-40.0
42.5-45.0
45.0-47.5
47.5-49.5
50.0-52.5
52.5-55.0
55.0-57.5
57.5-60.0

pollen was extremely poor throughout the series of samples, consequently, a reliable determination of tree pollen types was limited to the two taxa *Pinus sylvestris* and *Alnus glutinosa,* which are represented within the current native British flora (Clapham, Tutin and Warburg, 1962, 1987).

ZONATION OF THE FOSSIL POLLEN RECORD

The relative changes in representation of the taxa *Pinus sylvestris* and *Alnus glutinosa* from the sedimentary succession are described by the author in terms of local pollen assemblage zones, based upon the findings reported by Dr R. Bradshaw. These zones are defined in Table 34 and prefixed with an abbreviated site designation LMR denoting Loch Morar. Furthermore, the zones are numbered and cited in Table 34 in the sequence P1, P2 and P3 respectively, i.e. from oldest to youngest as they occur in the sedimentary succession. Appropriate comparisons have also been made by the author with published fossil pollen data from other locations in Scotland.

A POTENTIAL MODEL OF TIME VERSUS DEPTH FOR SEDIMENT CORE 2 FROM LOCH MORAR

A potential model of time versus depth was constructed for the top 60 centimetres of sediment core 2 from Loch Morar. This model incorporated data derived from the palaeomagnetic secular variation record and the fossil tree pollen record from sediment core 2. Table 35 cites the data which were used to construct the model.

The data for age (in years BP) versus depth in the sediment core (in centimetres) were processed by computer and fitted with regression curves of different orders of polynomials, which were tested for several statistical parameters, including the f-test. The y-variable (depth) was statistically weighted with 1 standard error (1σ), while the x-variable (time) was assumed to be constant. The statistical data derived for a first order (linear) polynomial, a third order (cubic) polynomial, and a fourth order (quartic) polynomial curve, respectively, are cited in Table 36. The different polynomial curves were fitted to these data by minimizing the least squares *sensu* Smith and Creer (1986). The author wishes to acknowledge the kind assistance of colleague, Dr Quentin Parker, University of Saint Andrew's, Scotland, who processed these data using main-frame computing facilities at the University of Edinburgh.

On the basis of the derived statistical data, a first order (linear) polynomial curve, and a fourth order (quartic) polynomial curve respectively, were fitted to

Table 34 - Zonation of the fossil pollen record from Loch Morar

Zone LMR-P1 (49.0-42.5cm)

Description: *Pinus sylvestris* pollen was represented at the lower boundary of this zone, subseqently increasing in abundance to attain an overall maximum in the fossil record between 49.0 and 45.0cm depth in the core. The lower boundary of this zone represents the base of the fossil pollen record in the sediment core

Age: Sediment depth 50.0-47.5cm correlates with the nrm record declination feature H (eta), which is dated from the European Holocene geomagnetic type-curves at 7,400 years BP (Creer and Tucholka, 1982a)

Other occurrences: Fossil pollen assemblages with high values of *Pinus* pollen, with *Betula* and *Corylus* are indicated from Loch Maree (lower boundary dated at 8,250±100 radiocarbon years BP (Q-1008), Birks, H.H., 1972a) and Loch Scionascaig (lower boundary dated at 7,880±160 radiocarbon years BP (Y-2364), Stuiver, 1969) and Loch Clair (Pennington *et al.*, 1971). High values of *Pinus* pollen with *Betula* and *Corylus* are indicated in peat from Loch Mor, Soay, near Skye, preserved beneath sediments containing high values of *Alnus glutinosa* pollen and fossil marine diatoms (Blackburn, 1940; Heslop-Harrison, 1948). A pollen record from the south basin of Loch Lomond indicates high values of *Pinus* pollen which correlate approximately with the nrm declination feature H (Dickson *et al.*, 1978), which is dated at 7,400 years BP

Zone LMR-P2 (42.5-35.0cm)

Description: *Alnus glutinosa* pollen is represented at the lower boundary of this zone. *Pinus sylvestris* pollen is also represented throughout this zone

Age: Sediment depth 42.5 to 40.0cm correlates with the nrm declination feature Z (zeta), which is dated from the European Holocene geomagnetic type-curves at 6,300 years BP (Creer and Tucholka, 1982a)

Other occurrences: Fossil pollen assemblages with *Alnus glutinosa* pollen values at 10 *per cent* or more are indicated from Loch Maree (lower boundary dated at 6,513±65 radiocarbon years BP (Q-1007), Birks, H.H., 1972a) and at Loch Clair (lower boundary dated at 6,520 radiocarbon years BP) and at Loch Scionascaig (dated at 6,250±140 radiocarbon years BP (Y-2363), Stuiver, 1969). The expansion of *Alnus glutinosa* indicated at Lochan Doilead is dated at 6,250 radiocarbon years BP (Williams, 1977; Birks, H.J.B., 1977). A pollen record from Loch Lomond indicates an increase in *Alnus* pollen values which correlates with the nrm declination feature Z (Dickson *et al.*, 1978), which is dated at 6,300 years BP

Zone LMR-P3 (35.0-0cm)

Description: *Pinus sylvestris* pollen exhibits a marked decrease in representation at the lower boundary of this zone. *Alnus glutinosa* pollen is represented throughout this zone. The upper boundary represents the top of the sedimentary succession and the fossil pollen record in the sediment core

Age: Sediment depth 35.0 to 32.5cm correlates with the nrm record declination feature E (epsilon) which is dated from the European Holocene geomagnetic type-curves at 4,200 years BP (Creer and Tucholka, 1982a)

Other occurrences: Fossil pollen assemblages which indicate sharply decreasing values of *Pinus* pollen are widely reported from a number of localities in northwestern Scotland. At Loch Maree, the decline in *Pinus* pollen values, to generally less than 10 *per cent*, is dated at 4,206±55 radiocarbon years BP (Q-1005) (Birks, H.H., 1972a). Furthermore, *Alnus glutinosa* and *Betula* probably represented the most abundant trees, while *Calluna vulgaris* and *Corylus/Myrica* comprised the most abundant pollen types, with values generally between 15 and 20 *per cent* (Birks, H.H., 1972a). A similar pollen assemblage is probably also represented at Loch Scionascaig (lower boundary dated at 4,020±100 radiocarbon years BP (Y-2362), Stuiver, 1969).

these data; a first order polynomial was applied to data points IV to VI (Table 35), while a fourth order polynomial was applied to data points I to VI, inclusively.

The polynomial least squares method provides an array of co-efficients, which can be used in conjunction with the appropriate algebraic expression, to calculate an unknown value of (y) for a known value of (x). A set of worked examples is presented in Table 37 which indicates the derivation of an unknown (y), using the three different orders of polynomials which were applied to the data from Loch Morar core 2.

Figure 21 illustrates a graph of age versus depth data, with the linear fit indicated by a continuous line, and the quartic fit indicated by an interrupted curve. The depth ranges are represented by crosses, while the mean depths are denoted by small boxes within the respective depth ranges.

The statistical tests indicate that the first order (linear) polynomial fit provides valid data for an unknown variable of either age (x) or depth (y) within the data range 33.75 to 47.00 centimetres and 4,200 to 8,250 years BP, respectively. The multiple linear correlation co-efficient (r) equals 0.99999. The intersection of the curve on the y-axis corresponds with a depth of 20.02 centimetres, which coincides with the base of the uppermost limnic mud in the sediment core, suggesting that the limnic mud is an unconsolidated sediment.

Outwith the data range covered by the first order (linear) polynomial fit, the fourth order (quartic) polynomial fit best represents the loci of these data, within the data range 12.50 to 47.00 centimetres and 1,200 to 8,250 years BP, respectively. The multiple linear correlation co-efficient (r) equals 0.99998. Thus, an unknown value of depth (y) may be interpolated directly from Figure 21 within the specified data range, or alternatively, it may be determined using the respective arrays of co-efficients for the polynomial curves.

A comparison between the observed depth ranges of the nrm secular variation features and the expected depth ranges ± 1σ, computed from the arrays of polynomial co-efficients, is indicated in Table 38.

The consistency of the observed nrm secular variation data presented in Table 38, with the time versus depth model for the top 60 centimetres of sediment core 2 from Loch Morar is illustrated in Figure 22.

The arrays of coefficients derived from the time versus depth model were used to determine the age of the lithostratigraphic transitions represented in the upper 50 centimetres of sediment core 2 from Loch Morar. These computed data are presented in Table 39.

Table 35 - Data used to construct a potential model of time versus depth for sediment core 2 from Loch Morar

Datum Point	y-variable Depth range in core (cm)	Mean depth in core (cm)	x-variable Age (years BP)	Data Source	Symbol in Figures
I	7.5-17.5	12.50	1,200	magnetic	B
II	17.5-22.5	20.00	2,000	magnetic	Γ
III	22.5-25.0	23.75	2,500	magnetic	Δ
IV	32.4-35.0	33.75	4,200	fossil pollen	P3
V	40.0-42.5	41.25	6,500	fossil pollen	P2
VI	45.0-49.0	47.00	8,250	fossil pollen	P1

Table 36 - Statistical data relating to the polynomial least squares curves

(1) *First Order (linear) Polynomial Least Squares Curve*

where $y = mx + c$

Array of co-efficients of the polynomial:	m = -3.26351 c = -20.01696 (constant)
Standard deviation of constant co-efficient	3.23723
Array of standard deviations of co-efficients	0.53824
Array of linear correlation co-efficients	-0.99999
Multiple linear correlation co-efficients (r)	0.99999
Reduce chi-square of fit	1.93896 x 10^{-4}
Value of f-test of fit	190182.56904

(2) *Third Order (cubic) Polynomial Least Squares Curve*

where $y = ax + bx^2 + cx^3 + d$

Array of co-efficients of the polynomial:	a = -15.10696 b = 1.90784 c = -9.91626 x 10^{-2} d = 3.50857 (constant)
Standard deviation of constant co-efficients:	6.59259 1.38772 9.12158 x 10^{-2}
Array of linear correlation co-efficients:	-0.98303 -0.93897 -0.88423
Multiple linear correlation co-efficient (r)	0.99991
Reduced chi-square of fit	1.72552 x 10^{-2}
Value of f-test of fit	3697.70555

(3) *Fourth Order (quartic) Polynomial Least Squares Curve*

where $y = ax + bx^2 + cx^3 + dx^4 + e$

Array of co-efficients of the polynomial:	a = -11.66819 b = 0.66751 c = 8.11487 x 10^{-2} d = -9.07412 x 10^{-3} e = 0.30125 (constant)
Standard deviation of constant co-efficient	20.60106
Array of standard deviations of co-efficients:	20.86077 7.28401 1.04350 5.23127
Array of linear correlation co-efficients:	-0.98303 -0.93897 -0.88423 -0.82884
Multiple linear correlation co-efficient (r)	0.99999
Reduced chi-square of fit	4.42230 x 10^{-3}
Value of f-test of fit	10822.63927

Table 37 - The derivation of an unknown variable (y) using co-efficients from different orders of polynomial least squares curves

(1) *First Order (linear) Polynomial Least Squares Curve*

For a known value of x (age) the corresponding value of y (depth) may be found according to the equation:

$$y = mx + c$$

If $x = 6.5 \times 10^3$ years BP, then the value of y will be:-

$y = (3.268 \times 6.5) + 20.02 \quad \therefore \quad y = 41.24$

$y = 41.24\ \text{cm} \pm 1\sigma \quad \therefore \quad y - 41.24 \pm 0.71\ \text{cm}$ $\quad (r = 0.99999)$

NB The linear polynomial curve was applied only to data within the following ranges: $x = 4.2 \times 10^3$ to 8.25×10^3 years BP, and $y = 33.75$ to 47.00 cm in depth

(2) *Third Order (cubic) Plynomial Least Squares Curve*

For a known value of x (age) the corresponding value of y (depth) may be found according to the equation:

$$y = ax + bx^2 + cx^3 + d$$

If $x = 6.5 \times 10^3$ years BP, then the value of y will be:-

$ax = -15.1070 \times 6.5 \quad = -98.1955$
$bx^2 = 1.9078 \times 6.5^2 \quad = 80.6045$
$cx^3 = (-9.9163 \times 10^{-2}) \times 6.5^3 \quad = -27.2326$
$d = 3.5086 \quad = 3.5086$

$\Sigma = -41.315 \quad \therefore \quad y = -41.32$

$y = 41.32\ \text{cm} \pm 1\sigma \quad \therefore \quad y = 41.32 \pm 2.67\ \text{cm}$ $\quad (r = 0.99999)$

(3) *Fourth Order (quartic) Polynomial Least Squares Curve*

For a known value of x (age) the corresponding value of y (depth) may be found according to the equation:

$$y = ax + bx^2 + cx^3 + dx^4 + e$$

If $x = 6.5 \times 10^3$ years BP, then the value of y will be:-

$ax = -11.6682 \times 6.5 \quad = -75.8433$
$bx^2 = 0.6675 \times 6.5^2 \quad = 22.2019$
$cx^3 = (8.1149 \times 10^{-2}) \times 6.5^3 \quad = 22.2850$
$dx^4 = (-9.0741 \times 10^{-3}) \times 6.5^4 \quad = -16.198$
$e = 0.3012 \quad =0.3012$

$\Sigma = -41.253 \quad \therefore \quad y = -41.25\ \text{cm}$

$y = 41.25\ \text{cm} \pm 1\sigma \quad \therefore \quad y = 41.25 \pm 2.67\ \text{cm}$ $\quad (r = 0.9999)$

Fig.21 A time versus depth model for Loch Morar sediment core 2 derived from n.r.m. and fossil pollen data

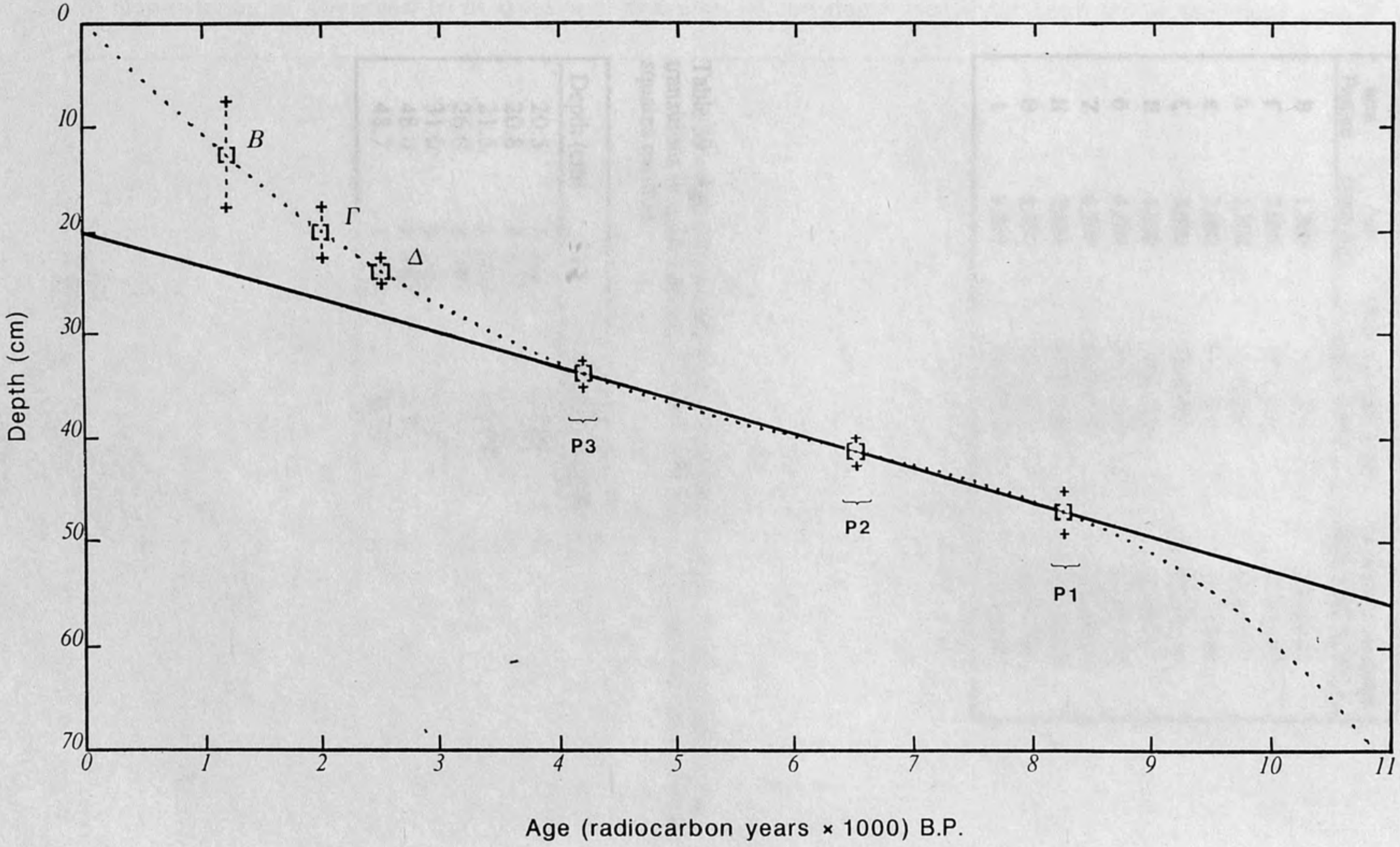


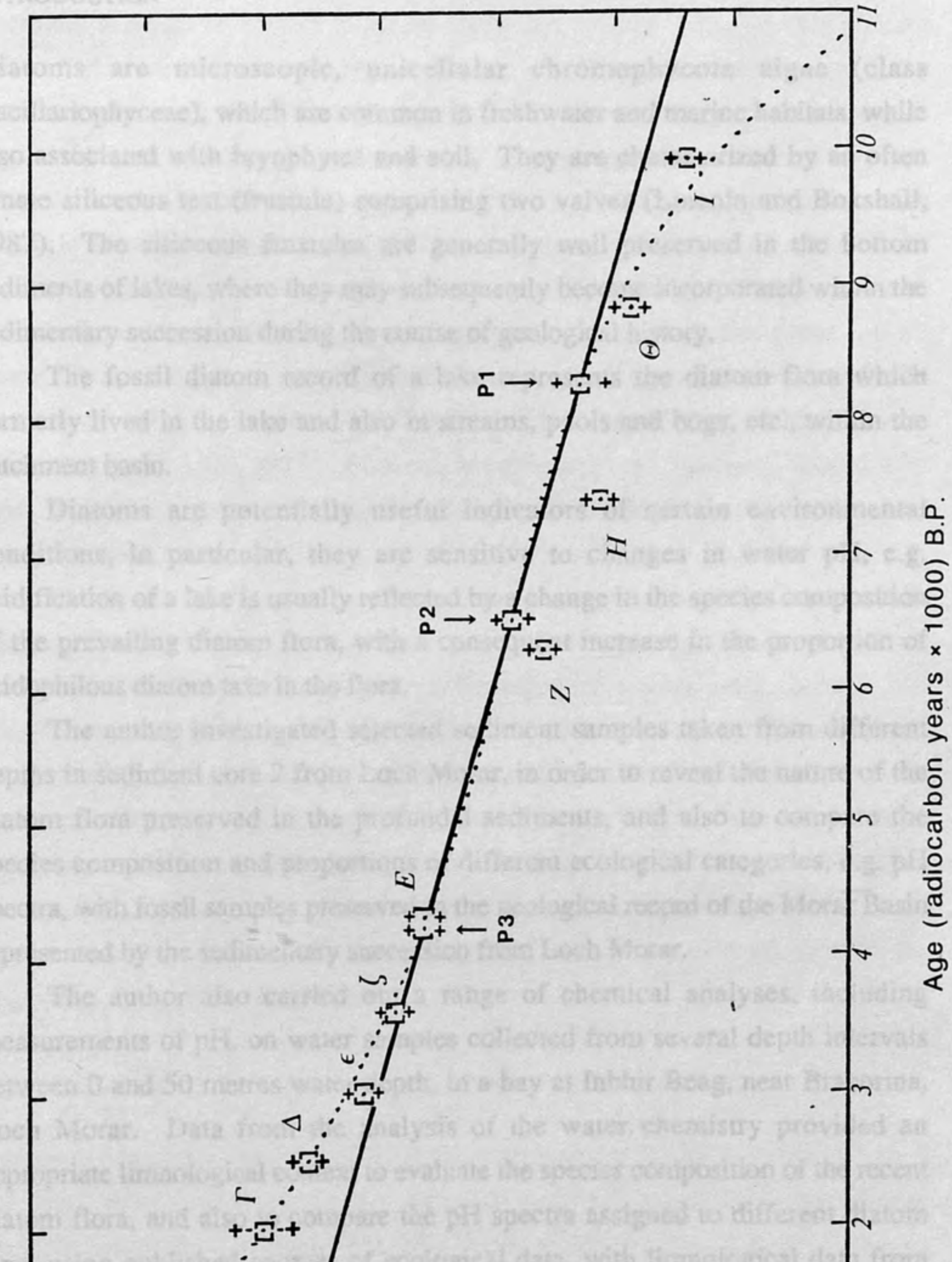
Table 38 - A comparison between observed and expected depth ranges of nrm declination and inclination features for Loch Morar sediment core 2

nrm Feature	Age (years BP)	Observed depth range in core 2 (cm)	Expected depth range (cm) ± 1σ in core 2
B	1,200	7.5-17.5	12.6±2.67
Γ	2,000	17.5-22.5	19.9±2.67
Δ	2,500	22.5-25.0	23.8±2.67
ε	3,000	27.5-30.0	27.2±2.67
ζ	3,600	30.0-32.5	30.8±2.67
E	4,200	32.5-35.0	33.7±0.71
ϑ	4,500	35.0-37.5	34.7±0.71
Z	6,300	42.5-45.0	41.2±0.71
H	7,400	47.5-50.0	43.8±2.67
Θ	8,800	50.0-52.5	49.8±2.67
I	9,900	55.0-57.5	58.3±2.67

Table 39 - Age determinations in years BP computed for lithostratigraphic transitions in sediment core 2 from Loch Morar, using the polynomial least squares method

Depth (cm)	±1σ	Age (Years BP)
20.5	± 2.67	2,080
20.8	± 2.67	2,110
21.5	± 2.67	2,200
26.0	± 2.67	2,810
31.0	± 2.67	3,640
48.0	± 2.67	8,560
48.7	± 2.67	8,590

Fig.22 Consistency of observed n.r.m. data with the time versus depth model for Loch Morar sediment core 2



THE FOSSIL DIATOM RECORD FROM THE LOCH MORAR SEDIMENTARY SUCCESSION

INTRODUCTION

Diatoms are microscopic, unicellular chromophycote algae (class Bacillariophyceae), which are common in freshwater and marine habitats, while also associated with bryophytes and soil. They are characterized by an often ornate siliceous test (frustule) comprising two valves (Lincoln and Boxshall, 1987). The siliceous frustules are generally well preserved in the bottom sediments of lakes, where they may subsequently become incorporated within the sedimentary succession during the course of geological history.

The fossil diatom record of a lake represents the diatom flora which formerly lived in the lake and also in streams, pools and bogs, etc., within the catchment basin.

Diatoms are potentially useful indicators of certain environmental conditions, in particular, they are sensitive to changes in water pH, e.g. acidification of a lake is usually reflected by a change in the species composition of the prevailing diatom flora, with a consequent increase in the proportion of acidophilous diatom taxa in the flora.

The author investigated selected sediment samples taken from different depths in sediment core 2 from Loch Morar, in order to reveal the nature of the diatom flora preserved in the profundal sediments, and also to compare the species composition and proportions of different ecological categories, e.g. pH spectra, with fossil samples preserved in the geological record of the Morar Basin represented by the sedimentary succession from Loch Morar.

The author also carried out a range of chemical analyses, including measurements of pH, on water samples collected from several depth intervals between 0 and 50 metres water depth, in a bay at Inbhir Beag, near Bracorina, Loch Morar. Data from the analysis of the water chemistry provided an appropriate limnological context to evaluate the species composition of the recent diatom flora, and also to compare the pH spectra assigned to different diatom taxa, using published sources of ecological data, with limnological data from Loch Morar.

RESULTS OF CHEMICAL ANALYSIS OF WATER SAMPLES FROM LOCH MORAR

Data from the analysis of twelve different inorganic solute concentrations and pH measurements of water samples from Loch Morar are presented in Table 40.

Measurements of the pH of water samples collected from an anchorage due west of Inbhir Beag in Loch Morar indicate that the water is approximately circum-neutral (sample mean pH=7.05) in this region of the loch. Furthermore, chemical analysis of twelve different inorganic solutes indicates that sodium (Na^+) forms the major cation, while chlorine (Cl^-) forms the major anion in the water samples analysed. The concentration of ionic sodium (sample mean = 5.87 $mgdm^{-3}$) may, however, be influenced by the proximity of the loch to the sea. The concentration of calcium carbonate ($CaCO_3$) measured by titration with ethylene diamine tetra acetic acid (EDTA) is extremely low (sample mean = 9.07 $mgdm^{-3}$), which reflects the non-calcareous nature of the Moine series rocks of the catchment area. Indeed, the solute concentrations of the water are all extremely low despite the prevailing oceanic climate (i.e. cool summers and mild winters) and high mean annual precipitation of between 2,000-2,500 millimetres (Climatological Atlas, 1952). Low solute concentrations, however, accord with slow weathering processes typically associated with metamorphic rock in the catchment area.

In view of the fact that the climate and geology interact to affect the soils and vegetation cover in the catchment area, it necessarily follows that these interactions will be reflected within the limnological environment. Indeed, it is possible that increasing acidification, indicated in the limnological environment by the prevailing diatom flora, may reflect changes in the chemistry of the soils in the catchment area and vegetation cover. The author investigated the fossil diatom record preserved in the sedimentary succession from Loch Morar, with the aim of determining, in particular, the pH spectra of diatoms represented in the fossil record and its possible palaeoenvironmental significance in relation to the vegetation cover of the Morar Basin .

METHOD OF SAMPLING AND PREPARATION FOR FOSSIL DIATOM ANALYSIS

Sediment samples were selected by the author from Loch Morar sediment core 2 for fossil diatom analysis from a series of depths cited in Table 41. These samples originally comprised part of a series which were subjected to various palaeomagnetic analyses, and also subjected to fossil pollen analysis, described previously. Thus, direct comparisons are possible between various data pertaining to specific samples. The sample depths cited refer to depth below the top of the sedimentary succession, i.e. relative to zero datum in core 2.

The respective sample depths have been dated according to the potential time versus depth model for Loch Morar sediment core 2, described previously in this chapter. These age determinations are presented in Table 42.

Table 40 - Solute concentrations (in mgdm^{-3}) of water sampled from 0-50 metres depth, near Bracorina, Loch Morar

Water depth (m)	pH	$CaCO_3$	Cl^-	Na^+	K^+	SiO_2	NH_4^+	PO_4^{3-}	NO_3^-	NO_2^-	Al^{3+}	Fe^{3+}	Mn^{2+}
1	7.10	8.0	8.0	5.9	0.15	1.125	0.08	<0.02	<1.0	<0.002	<0.01	<0.01	<0.005
5	7.10	9.0	8.0	5.9	0.15	1.125	0.08	<0.02	<1.0	<0.002	<0.01	<0.02	<0.005
10	6.80	8.0	8.0	5.9	0.15	1.075	0.10	<0.02	<1.0	<0.002	<0.01	<0.01	<0.005
20	7.05	9.0	8.0	5.9	0.15	1.200	0.10	<0.02	<1.0	<0.002	<0.01	<0.015	<0.005
30	7.20	10.0	8.0	5.7	0.15	1.050	0.10	<0.02	<1.0	<0.002	<0.01	<0.01	<0.005
40	6.85	9.5	8.0	5.9	0.15	1.250	0.10	<0.02	<1.0	<0.002	<0.01	<0.01	<0.005
50	7.25	10.0	8.0	5.9	0.15	1.220	0.10	<0.02	<1.0	<0.002	<0.01	<0.01	<0.005

Table 41 - Sediment sample depths selected in Loch Morar sediment core 2 for fossil diatom analysis

Sample depth (cm)	*Sediment description*	*Notes regarding fossil diatom content of sample*
0.5	Lacustrine mud (7.5YR4/4-2)	Fossils well preserved
6.0	Lacustrine mud (7.5YR4/4-2)	Fossils well preserved
11.0	Lacustrine mud (7.5YR4/4-2)	Fossils well preserved
20.0	Lacustrine mud (7.5YR4/4-2)	Fossils well preserved
21.0	Silt (2.5Y5/4)	Only a few eroded fragments
23.0	Lacustrine mud with Iron (III) Oxide (7.5YR3/2-4/2)	Only a few diatom fragments
26.5	Lacustrine mud (7.5YR4/4)	Fossils well preserved
34.0	Lacustrine mud with silt (10YR5/5)	Fossils well preserved
46.5	Lacustrine mud with silt (10YR5/5)	Fossils well preserved
48.0	Silt (10YR5/6)	Fossils well preserved
48.5	Clay with silt (2.5Y7/0)	No fossil diatoms
49.0	Clay with silt and fine sand (5Y6/1)	Fossils well preserved
53.5	Clay with silt and fine sand (5Y6/1)	Fossils poorly preserved
55.0	Clay with silt and fine sand (5Y6/1)	Only a few eroded fragments
56.5	Clay with silt and fine sand (5Y6/1)	No fossil diatoms
58.5	Clay with silt and fine sand (5Y6/1)	No fossil diatoms
61.0	Clay with silt and fine sand (5Y6/1)	No fossil diatoms
66.5	Laminated clay (5Y5/3-5Y6/1)	No fossil diatoms
85.5	Laminated clay (5Y5/3-5Y6/1)	No fossil diatoms

Table 42 - Age determinations in years BP computed for the fossil diatom samples from Loch Morar sediment core 2

Depth (cm)	±1σ	Age (years BP)
0.5	+2.67	Present
6.0	±2.67	560
11.0	±2.67	1,040
20.0	±2.67	2,020
26.5	±2.67	2,890
34.0	±0.71	4,280
39.5	±0.71	5,960
46.5	±0.71	8,100
48.0	±2.67	8,460
49.0	±2.67	8,650
53.5	±2.67	9,350

SAMPLE PREPARATION

The sediment samples were prepared for diatom analysis using the procedures described by Haworth (1976) and West (1977), and augmented with additional methodology devised by the author, which is described below. Thus, a selected sediment sample measuring approximately 0.5 cubic centimetres was placed in a conical flask (250 cubic centimetres capacity) and treated with a few drops of 30 *per cent* Hydrogen Peroxide (H_2O_2), 10 cubic centimetres of 1 Normal solution of Potassium Dichromate ($K_2Cr_2O_7$) and mixed thoroughly. To this mixture was also added 20 cubic centimetres of concentrated Sulphuric acid (H_2SO_4), taking particular care to add this reagent slowly. The resulting chemical oxidation of the sediment was allowed to proceed for 30 minutes, within the confinement of a laboratory fume cupboard.

Approximately 15 cubic centimetres of the oxidized sediment preparation was then taken and centrifuged at 1000rpm for approximately 6 minutes, so that the orange coloured supernatant liquor became clear and non-turbid. The supernatant liquor was then discarded and distilled water was added to the pellet retained in the centrifuge tube, which was mixed thoroughly and centrifuged as indicated previously. This procedure was repeated twice and the pellet was retained; by this stage the supernatant liquor was clear and colourless.

The pellet was then added to a measuring cylinder (50 cubic centimetres capacity) with distilled water, which was made up to the volume, i.e. 50 cubic centimetres. This mixture was thoroughly shaken and a Pasteur pipette sample was quickly removed from a mid-point in the cylinder column. Three drops of the mixture were then pipetted onto a cleaned microscope coverslip (size 0) and left to dry in air in a horizontal position and in a vibration-free enclosure. Three drops of a high refractive index diatom mountant (Naphrax; RI=1.74) were pipetted on to a cleaned microscope slide, upon which a single coverslip with prepared sample was then inverted. The slide was then placed on a pre-heated electrical heating plate set at *circa* 70°C, and left for 30 seconds; during this period the mountant bubbled vigorously and then becomes coalescent and light straw coloured. After removal from the heating plate the coverslip was lightly pressed to the glass slide, thus forcing excess mountant to exude from the edges of the coverslip. Upon cooling, the thin layer of mountant beneath the coverslip generally set rapidly. Finally, the prepared slide was appropriately labelled and retained for subsequent microscopic examination.

The diatom identifications and fossil assemblage analysis were made under a Leitz Dialux microscope with a camera lucida facility, kindly provided by the Department of Botany, University of Edinburgh.

Each sample which contained well preserved diatom fossils was subjected to an average count of 500 diatom values encountered along a continuous traverse of the microscope slide.

The author wishes to acknowledge with gratitude the generous help and assistance of Dr Elizabeth Y. Haworth, Freshwater Biological Association, Windermere, along with Dr David G. Mann, Department of Botany, University of Edinburgh, who provided practical assistance with the diatom taxonomy and fossil identification of the Loch Morar samples. The author used taxonomic publications by Schmidt (1873-1959), Hustedt (1930-1966), Cleve-Euler (1951-1955), Haworth (1974) and Lange-Bertalot (1977) for the purposes of identifying the fossil diatom taxa. The taxonomic nomenclature and authorities have been checked where possible by the author, with invaluable help from Dr E.Y. Haworth (FBA, Windermere).

RESULTS OF THE MICROSCOPE ANALYSIS OF THE FOSSIL DIATOM SAMPLES

A cumulative list of 130 different fossil diatom taxa identified by the author from Loch Morar sediment core 2 is presented in Table 43. These taxa have been arranged in alphabetical order and assigned an individual taxon code for ease of description.

The frequency of occurrence of a particular taxon per counted sample from the sediment core is presented numerically in Table 44. This table is also arranged to indicate the range of individual diatom taxa recorded within each counted sample. Furthermore, the ecological data provided by Jørgensen (1948, 1950), Foged (1953, 1954, 1968, 1969), Round (1959), Florin (1970), Pennington *et al.* (1972) and Haworth (1976) have enabled the majority of diatom taxa to be grouped into the various categories within the pH, salinity, and current ecological habitat, pH and salinity spectra as defined by Foged (1954). The respective categories are indicated by an abbreviated notation which is described in Table 44.

The proportion of different current ecological habitat categories, i.e. limnophilous (including limnobiontic), indifferent, rheophilous (including rheobiontic), and planktonic fossil diatoms, represented within each counted sample is presented in Table 45.

The proportion of different pH categories, i.e. acidophilous (including acidobiontic), indifferent (circum-neutral) and alkaliphilous (including alkalibiontic) fossil diatoms represented within each counted sample is presented in Table 46.

The proportion of different salinity categories (halobion), i.e. halophilous, indifferent, and halopholous fossil diatoms, represented within each counted sample is presented in Table 49.

In cases where a taxon exhibits a shared affinity with two ecological categories, e.g. limnophilous/indifferent, the taxon count is entered as 0.5 in the respective categories.

These data are therefore indicative of changes in ecological preferences of the diatom assemblages, which can frequently be correlated with the lithostratigraphy and microfossil pollen record of the sediments.

Lakes which contain water with low concentrations of dissolved inorganic and organic solutes, pH values ranging from neutral to acidic (i.e. pH=7.0 or less), and low primary productivity, are often termed oligotrophic lakes. These lakes support a diatom flora which is generally distinct from eutrophic lakes, which contain water with high concentrations of dissolved solutes, pH values which are often alkaline (i.e. pH >7.0), and relatively high primary productivity.

Data from the analysis of the water chemistry of Loch Morar, cited previously in Table 40, indicate that the current status of this loch corresponds with the definition of an oligotrophic lake. Furthermore, the most recent bottom sediments which have accumulated in the deep profundal zone of the loch contain diatom taxa that are particularly characteristic of oligotrophic lakes. In particular, the diatom flora typically includes a planktonic assemblage dominated by species of the genus *Cyclotella* along with *Melosira distans* and its varieties, while other representative taxa include the genera *Anomoeoneis, Frustulia, Eunotia* and *Tabellaria.*

In contrast, planktonic diatom assemblages that are usually indicative of eutrophic lakes, include the taxa *Fragilaria crotonensis, Melosira granulata, M. ambigua, M. islandica* spp. *helvetica, Stephanodiscus dubius, S. hantzschia, S. astraea, S. astraea* var. *minutula* and *Asterionella formosa.* None of these taxa were recorded by the author from the analysis of the diatom samples from Loch Morar.

The lowest sample depth in sediment core 2 from Loch Morar which contained sufficiently abundant diatom values to permit a count of 500 microfossils occurred at 53.5 centimetres depth in the core. These microfossils were, however, poorly preserved in the clay with silt and fine sand. A sample taken from 1.5 centimetres depth beneath this point in the core, at 55.0 centimetres depth, yielded only a few eroded diatom fragments which were tentatively identified as girdle bands of genus *Pinnularia,* while samples taken from the laminated clay and fine sand, occurring below 64.5 centimetres depth in the core yielded no fossil diatoms. These laminated minerogenic sediments core,

Table 43 - The cumulative list of fossil diatom taxa from Loch Morar core 2

Taxon Code	Taxon
I	*Achnanthes flexella* (Kutzing 1844) Brun 1880
2	*Ac. lanceolata* (Brébisson 1849) Grunow 1880
3	*Ac. lanceolata* var. *elliptica* Cleve 1891
4	*Ac. linearis* (Wm. Smith 1855) Grunow 1880
5	*Ac. marginulata* Grunow 1880
6	*Ac. microcephala* (Kutzing 1844) Grunow 1881
7	*Ac. minutissima* Kutzing 1833
8	*Ac. pusilla* (Grunow 1880) de Toni 1891
9	*Amphora ovalis* var. *libyca* (Ehrenberg 1840) Cleve 1894
10	*Am. veneta* Kutzing 1844
11	*Am. veneta* var. *capitata* Haworth 1974
12	*Amphora* sp.
13	*Anomoeoneis exilis* (Kutzing 1844) Cleve 1891
14	*An. exilis* var. *laneolata* Mayer 1919
15	*An. serians* var. *brachysira* (Brébisson 1853) Cleve 1882
16	*Cocconeis diminuta* Pantocsek 1902
17	*Coc. placentula* Ehrenberg 1838
18	*Coc. placentula* var. *euglypta* (Ehrenberg 1854) Grunow 1884
19	*Coc. placentula* var. *klinoraphis* Geitler 1927
20	*Coc. placentula* var. *lineata* (Ehrenberg 1841) Van Heurck 1885
21	*Coc. thienemanni* Hustedt 1954
22	*Cyclotella bodanica* Eulenstein 1878
23	*Cyc. kuzingiana* Thwaites 1848
24	*Cyc.* ref. *stelligeroides* Hustedt 1945
25	*Cymbella affinis* Kutzing 1844
26	*Cym. angustata* (Wm. Smith 1853) Cleve 1894
27	*Cym. cesatii* (Rabenhorst 1853) Grunow 1881
28	*Cym. cistula* (Hemprich 1828) Kirchner 1878
29	*Cym. cymbiformis* Agardh 1830
30	*Cym. delicatula* Kutzing 1849
31	*Cym. laneolata* (Agardh 1830; Ehrenberg 1838) Van Heurck 1880
32	*Cym. lunata* Wm. Smith 1855
33	*Cym. microcephala* Grunow 1881
34	*Cym. naviculiformis* Auerswald in Rabenhorst 1861
35	*Cym. parva* (Wm. Smith 1853) Wolle 1890
36	*Cym. perpusilla* A. Cleve 1895
37	*Cym. pusilla* Grunow 1875
38	*Cym. turgida* Gregory 1856
39	*Cym. ventricosa* (Kutzing 1833) Kutzing 1844
40	*Cymbella* sp.
41	*Denticula tenuis* Kutzing 1844
42	*Den. tenuis* var. *crassula* (Naegeli 1849) Hustedt 1930
43	*Diatoma elongatum* (Lyngbye 1819) Agardh 1924
44	*Didymosphenia geminata* (Lyngbye 1819) M.Schmidt 1899
45	*Epithemia sorex* Kutzing 1844
46	*Eunotia arcus* Ehrenberg 1838
47	*Eun. diodon* Ehrenberg 1837
48	*Eun. faba* (Ehrenberg 1854) Grunow 1881
49	*Eun. lunaris* (Ehrenberg 1831) Brébisson 1864
50	*Eun. lunaris* var. *subarcuata* (Naegeli 1849) Grunow 1881
51	*Eun. meisteri* Hustedt 1930
52	*Eun. monodon* Ehrenberg 1841
53	*Eun. pectinalis* (Dillwyn 1783) Rabenhorst 1864
54	*Eun. pectinalis* var. *minor* (Kutzing 1844) Rabenhorst 1864
55	*Eun. pectinalis* var. *entralis* (Ehrenberg 1841) Hustedt 1911
56	*Eun. tenella* (Grunow 1881) Hustedt 1913
57	*Eun. trinacria* Krasske 1929
58	*Eun. valida* Hustedt 1930
59	*Fragilaria* ref. *atomus* Hustedt 1931

60 *F. capucina* Desmazieres 1825
61 *F. capucina* var. *lanceolata* Grunow 1881
62 *F. construens* (Ehrenberg 1841) Grunow 1862
63 *F. construens* var. *binodis* (Ehrenberg 1843) Grunow 1862
64 *F. construens* var. *subsalina* Hustedt 1925
65 *F. construens* var. *venter* (Ehrenberg 1854) Grunow 1881
66 *F. vaucheriae* (Kutzing 1833) Petersen 1938
67 *F. pinnata* Ehrenberg 1841
68 *F. virenscens* Ralfs 1843
69 *Fragilaria* sp.
70 *Frustulia rhomboides* (Ehrenberg 1841) de Toni 1891
71 *Frus. rhomboides* var. *saxonica* (Rabenhorst 1851) de Toni 1891
72 *Gomphonema acuminatum* Ehrenberg 1832
73 *G. acuminatum* var. *coronata* (Ehrenberg 1840) Wm. Smith 1853
74 *G. acuminatum* var. *pusillum* Grunow 1880
75 *G. angustatum* (Kutzing 1844) Rabenhorst 1864
76 *G. gracile* Ehrenberg 1838
77 *G. gracile* var. *auritum* (Braun *in litt.*, Kutzing 1849) Van Heurck 1880-1885
78 *G. intricatum* Kutzing 1844
79 *G. intricatum* var. *dichotum* (Kutzing 1833, 1834) Grunow 1880
80 *G. intricatum* var. *pulvinatum* (Braun 1853) Grunow 1880
81 *G. montanum* var. *subclavatum* Grunow in Van Heurck 1885
82 *G. olivaceum* var. *minutissima* Hustedt 1930
83 *G. parvulum* (Kutzing 1844) Kutzing 1849
84 *Melosira distans* ref. var. *alpigena* Grunow 1882
85 *Melosira* sp.
86 *Navicula acceptata* Hustedt 1950
87 *N. cari Ehrenberg* 1836
88 *N. cincta* (Ehrenberg 1854) Ralfs 1861
89 *N. cocconeiformis* Gregory 1856
90 *N. jarnefeltii* Hustedt 1936
91 *N. lapidosa* Krasske 1929
92 *N. perpusilla* Grunow 1860
93 *N. pseudoclamans* Carter 1981
94 *N. pseudoscutiformis* Hustedt 1930
95 *N. pupula* Kutzing 1844
96 *N. radiosa* Kutzing 1844
97 *N. radiosa* var. *tenella* (Brébisson 1849) Van Heurck 1881
98 *N. schonfeldii* Hustedt 1930
99 *N. scutiformis* Grunow 1881
100 *Navicula* sp.
101 *Neidium bisulcatum* (Lagerstedt 1873) Cleve 1891
102 *Nitzschia acidoclinata* Lange-Bertalot 1977
103 *Ni. amphibia* Grunow 1862
104 *Ni. angustat* var. *acuta* Grunow 1880
105 *Ni. denticula* Grunow 1880
106 *Ni. fonticola* Grunow 1879
107 *Ni. frustulum* (Kutzing 1844) Grunow 1880
108 *Ni. hantzschiana* Rabenhorst 1860
109 *Nitzschia* sp.
110 *Opephora martyi* Heribaud 1902
111 *Peronia heribaudi* Brun et M. Peragallow 1893
112 *Pinnularia interrupta* Wm. Smith 1853
113 *P. microstauron* (Ehrenberg 1841) Cleve 1891
114 *P. molaris* (Grunow 1863) Cleve 1895
115 *P. nobilis* (Ehrenberg 1840) Ehrenberg 1841 (1843)
116 *P. obscura* Krasske 1932
117 *P. rupestris* Hantzsch ex Rabenhorst 1861
118 *P. stauroptera* (Grunow 1860) Rabenhorst 1864
119 *P. sublinearis* (Grunow in Van Heurck 1880-1884) Cleve 1894
120 *P. undulata* Gregory 1854
121 *P. viridis* (Nitzsch 1817) Ehrenberg 1841 (1843)
122 *Stauroneis prominula* (Grunow 1879) Hustedt 1959
123 *Surirella ovata* Kutzing 1844

124	*Synedra acus* Kutzing 1844
125	*Sy. acus* var. *angustissima* Grunow 1881
126	*Sy. acus* var. *radians* (Kutzing 1844) Hustedt 1930
127	*Sy. nana* Meister 1912
128	*Sy. ulna* (Nitzsch 1817) Ehrenberg 1838
129	*Tabellaria fenestrata* (Lyngbye 1817) Kutzing 1844
130	*T. flocculosa* (Roth 1797) Kutzing 1844

Table 44 - Count data of fossil diatoms from selected depths in Loch Morar core 2

Taxon	Ecological Spectra				Depth in Core 2 (cm)										
Code	pH	Salt	Ecol	PL	0.5	6.0	11.0	20.0	26.5	34.0	39.5	46.5	48.0	49.0	53.5
1	Ind	Ind	Lp		3	1		2	1	2	1				
2	Alp	Ind	Rb											1	
3	Alp	Ind	Rb											1	
4	Ind	Ind	Ind								4	1			
5	Alp	Ind					2	1	1	1	1				
6	Ind	Ind	Ind		24	61	61	4	12	45	35	46	19	4	
7	Ind	Ind	Ind		57	57	55	15	31	67	72	32	41	2	
8										2	1		1		
9	Alp	Ind	Ind					1	1		1				
10	Alp	Ind						1							
11															1
12													1	1	
13	Ind	Ind	Ind		80	86	92	35	103	103	72	41	61	3	1
14	Ind	Ind	Ind								1				
15	Acp	Hb			10	22	20	21	23	19	5	9	21	10	
16	Alp	Hb	Ind						1		2			1	1
17	Alp	Ind	Ind			1									
18	Alp	Ind	Ind								1				
19	?Alp					1									
20	Alp	Ind	Ind							1					
21									1						
22	Ind	Ind		P									1		
23	Ind	Ind	Ind	P	103	80	53	72	68	60	88	89	101	42	16
24	Ind	Ind	Lp/Ind	P	182	64	113	285	117	80	130	245	194	399	454
25	Alp	Ind	Ind				1			1			1		
26	Ind	Ind							2	1					
27	Ind	Ind			1	1	1	1	1	3		1		1	
28	Ind	Ind	Lp										1		
29	Ind/Alp	Ind	Lb			1									
30	Alp	Ind			1	1					1		1		1
31	Alp	Ind													1
32	Ind	Ind	Rp		2	3	6		8	6		1	1	4	
33	Alp	Ind	Ind			2			1	7	2	1			
34	Ind	Ind	Ind		2										
35	Alp	Ind	Lp											1	
36	Acb	Hb							2			1			
37						4	2		1						
38	Alp	Ind	Lp				1			2				2	1
39	Ind	Ind	Ind			3	2	1	1	3	2	1	3	1	
40					1										
41	Alp	Hb					1					1			
42					3	1	1				2		3	1	
43	Ind/Alp	Hp		P							7				
44	Ind	Ind	Rp											1	
45	Alp	Ind	Lb											1	
46	Ind/Acp	Hb				3				3	2		1		
47	Acp	Hb						1							
48	Acp						1								
49	Ind/Acp	Ind					2		2	1					
50	Acp				1	2									
51	?Acp						1								
52	Acp	Hb	Lp											1	
53	Acp	Hb	Ind			1									
54	Acp	Hb	Ind		4			1	1	4			1		
55	Acp	Hb	Ind			1	1								
56	Acp	Hb				7		2	1	3	2			1	
57	?Acp								1						
58	Acp	Hb				1	2								
59		Ind				1									
60	Alp	Ind	Ind	P						1					
61		Ind		P			1				1		1		
62	Alp	Ind	Ind										5	4	2
63	Alp	Ind	Ind							2		2	2		

Taxon	Ecological Notes				Depth in Core 2 (cm)										
Code	pH	Salt	Ecol	PL	0.5	6.0	11.0	20.0	26.5	34.0	39.5	46.5	48.0	49.0	53.5
64	Alp	Ind						3						2	
65	Alp	Ind								1		2	2		
66	Alp	Ind	Ind		3			2					2		
67	Alp	Ind	Ind			1									
68	Ind	Hb	Ind		2	17	9	2	5	5	8	3	3	5	10
69										2	1				
70	Acp	Hb	Lp				1			1					
71	Acp	Hb	Lp			6	7	2	5	4	3		1		
72	Alp	Ind	Lp				1								
73	Alp	Ind	Lp						1	1	1				1
74													1		
75	Alp	Ind	Ind		1	1			2						
76	Ind/Alp	Ind	Lp			4	1		2	1	1	1		1	
77	Alp	Ind								2					
78	Alp	Ind	Lb				1						1	1	
79	Alp	Ind										1			
80						1									
81	Alp							1							
82						1									
83	Ind	Ind	Rp			2	1						1		
84	Acp	?Ind		P	13	29	38	42	83	43	42	8	13	5	7
85															1
86						1									
87	Alp	Ind	Rb						1	1					
88	Alp	Hp	Rp										1		
89	Acp	Hb	Rp			2	1		1	1				1	
90	Acp	Ind					1								1
91						1									
92	Ind	Ind				2									
93									1						
94	Ind	Ind	Ind		1	1				1					
95	Ind	Ind	Ind				1								
96	Ind	Ind	Ind				1				2				
97	Ind	Ind	Ind			2									
98	Alp	Ind				1							1		
99	Ind							1							
100												1			
101	Ind	Ind	Ind		2	1									
102									1						
103	Alp	Ind	Ind				2					1			
104	Alp	Ind	Lp				2	1					1		
105	Alp	Ind	Ind						1			1			
106	Alp	Ind	Ind									3			
107	Alp	Hp	Lb						1				1		
108	Ind/Acp	Ind			1							1	1		
109						2				1	3		1		1
110	Alp	Ind	Lp											2	1
111	Acp								1	1			1		
112	Acp	Ind	Ind		1	1				2					
113	Ind	Ind	Ind			1			1	1					
114	Ind	Ind						1							
115	Ind/Acp	Ind/Hb	Ind/Lp						1						
116									1	2					
117							2								
118						1									
119							2		1	1			1		
120	Acp	Ind											1		
121	Ind	Ind	Ind							1					
122	Ind	Hp							1						
123	Alp	Ind	Rp								1				
124	Alp	Ind			1										
125	Ind	Ind	Lp								1				
126	Alp	Ind		P		1				3	1	5	2		
127	Ind	Ind	Lp	P		1									
128	Alp	Ind	Ind										1		1
129	?Acp	Hb	Lb	P		10	8	2	5	4	1		3	1	
130	Acp	Hb	Ind	P	1	4	3		5	4	2	2	1		

The notation used in the tables of count data of fossil diatoms from Loch Morar core 2 is as follows:-

(i) Taxon code refers to the cumulative list of fossil diatom taxa (Table 43).

(ii) Ecological spectra (where available) for a given taxon have been abbreviated thus:-
pH Ind = Indifferent, i.e. Circum-neutral; Alp = Alkaliphilous;
Alb = Alkalibiontic;

Acp = Acidophilous; Acb = Acidobiontic

Salt (i.e. halobian tolerance) Ind = Indifferent; Hp = Halophilous;

Hb = Halophobous

Ecol. (i.e. current ecological habitat) Ind = Indifferent; Lp = Limnophilous;
Lb = Limnobiontic; Rp = Rheophilous; Rb = Rheobiontic
Pl = Planktonic

(iii) Definition of some epithets used in the ecological spectra descriptions

limno-	f.Gk. *limne* lake
rheo-	f.Gk. *rheos* stream
-philous	f.Gk. *phileõ* love
-phobous	f.Gk. *phobos* fear
-biontic	f.Gk. *bios* (course of) life

are interpreted by the author, on the basis of palaeomagnetic data, as representing material deposited in the loch during the glacial conditions probably associated with the Loch Lomond Stadial (*circa* 11,000 to 10,000 years BP). Significantly, the oldest diatom remains preserved in the sediments may not necessarily represent the earliest flora to have occurred in the Morar Basin. Indeed, studies in Norway and Iceland have revealed that diatoms occur in streams, pools, springs and flushes in the vicinity of current glaciers, while predominantly minerogenic material arising from glacier erosion is contemporaneously transported by meltwater streams and deposited downstream in rock basins, etc. (Haworth, 1976). Under these circumstances, the diatom frustules are generally well dispersed amongst the minerogenic contribution to the sedimentary succession. Furthermore, a relic diatom assemblage only starts to accumulate when the diatoms in the rock basins become sufficiently numerous, and when the supply and input of minerogenic sediment decreases, consequent upon the retreat of the glacier ice and a general stabilization of the landscape in the catchment area (Haworth, 1976).

The diatom taxa represented in all the samples analysed from sediment core 2 from Loch Morar were in descending order of abundance, as follows: *Cyclotella* ref. *stelligeroides, C. kutzingiana, Anomoeoneis exilis* and *Melosira distans* var. *alpigena*. These were followed in turn by *Achnanthes minutissima, A. microcephala* and *Anomoeoneis serians* var. *brachysira*, which were recorded in all the samples analysed, with the exception of the sample taken from 53.5 centimetres depth in the sediment core.

The taxa *Cyclotella stelligeroides* and *C. kutzingiana* are planktonic in habit, while *Anomoeoneis exilis, Achnanthes minutissima* and *A. microcephala* are described as having indifferent ecological spectra. The taxon *Melosira distans* var. *alpigena* is planktonic and acidophilic, while *Anomoeoneis serians* var. *brachysira* is acidophilic and halophobic in affinity.

The planktonic element of the diatom flora is dominant in all the samples analysed. This trend is indicated by data relating to the proportion of different current ecological categories of fossil diatoms in core 2, which are presented in Table 45. Furthermore, the dominant planktonic diatoms belong to the genus *Cyclotella,* which tend to be found in water of neutral pH (±7) (Haworth, 1976) This is consistent with pH data of water samples from Loch Morar. *Cyclotella* plankton are cited as being characteristic of oligotrophic lakes of the northern sub-alpine and temperate zones (Hustedt, 1937-1939). The abundance of *Cyclotella* spp. in the fossil record from Loch Morar, suggests that this genus represented a characteristic part of the plankton flora, following the cessation of glacial conditions associated with the Loch Lomond Stadial, and continued thereafter to

Table 45 - The proportion of different current ecological habitat categories of fossil diatoms represented in Core 2

Depth in Core 2 (cm)	Lp No	%	Ind No	%	Unknown No	%	Rh No	%	No. of taxa Types	Σ	Planktonic No	%	Types
0.5	94	18.8	342	68.4	62	12.4	2	0.4	25	500	299	59.8	4
6.0	55	11.0	353	70.7	84	16.8	7	1.4	49	499	189	37.9	7
11.0	78.5	15.7	337.5	67.4	77	15.4	8	1.6	39	501	216	43.1	6
20.0	149.5	29.9	275.5	55.1	75	15.0	0	0.0	25	500	401	80.2	4
26.5	74.5	14.9	292	58.4	123.5	24.7	10	2.0	42	500	278	55.6	5
34.0	55	11.0	348	69.6	89	17.8	8	1.6	45	500	195	39.0	7
39.5	73	14.6	357	71.4	69	13.8	1	0.2	35	500	272	54.4	8
46.5	123.5	24.7	345.5	69.1	30	6.0	1	0.2	26	500	349	69.8	5
48.0	105	21.0	338	67.6	54	10.8	3	0.6	41	500	316	63.2	8
49.0	209.5	41.9	261.5	52.3	21	4.2	8	1.6	29	500	447	89.4	4
53.5	230	45.9	258	51.5	13	2.6	0	0.0	17	501	477	95.2	3

be a significant component in the diatom flora during the Holocene Epoch. Loch Morar, therefore, corresponds to the definition of a *Cyclotella* lake *sensu* Hustedt (1937-1939), i.e. oligotrophic in status.

The contribution of the planktonic element to the fossil record represented in core 2 is possibly accentuated, due to the location of the core site beneath deep water (61 metres) in the profundal zone of the loch, i.e. below the level of effective light penetration. Indeed, the contribution of diatoms typically associated with the shallower littoral zone is only slight, although some taxa of the genus *Fragiliaria* are sporadically represented in the fossil record.

Although the representation of *Fragilaria* spp. in the record from Loch Morar is generally rare, the restricted presence of *Fragilaria construens* in the lower part of the succession analysed, i.e. between 48.0 to 53.5 centimetres depth in core 2, is nevertheless significant. Diatoms of the genus *Fragilaria* tend to be found in alkaline waters (Haworth, 1976). Indeed, *Fragilaria construens* and *F. construens* var. *venter* were prominent in a list of 74 diatom taxa recorded in 1968 on the volcanic island of Surtsey, situated off the coast of Iceland, following its inception in 1963 (Behre and Schwabe, 1970). These taxa were also among the first to appear in many Late Devensian Lateglacial diatom assemblages, e.g. at Kentmere, in the Cumbrian Lake District, England (Round, 1957), Bølling So in Denmark (Fjerdingstad, 1954), in Pickerel Lake (Haworth, 1972) and Kirchner Marsh (Florin, 1970) in North America, and in Loch Scionascaig (Pennington *et al.*, 1972), Loch Borralan and Cam Loch (Haworth, 1976) in northern Scotland.

The maximum representation of *Fragilaria construens* in the lower part of the fossil record from Loch Morar, i.e. at 48.0 centimetres depth in sediment core 2, corresponded with a layer of silt containing detrital organic Carbon including microfossil pollen of *Pinus sylvestris*, which is interpreted by the author as representing material deposited in the loch during the early part of the Holocene Epoch (*post*-10,000 years BP). Other alkaliphilous diatom taxa represented in the lower part of the succession analysed, although generally rare, included *Achnanthes lanceolata* var. *elliptica, Cocconeis diminuta* and *Epithemia sorex.*

The proportion of different pH categories of fossil diatoms in core 2 are indicated in Table 46. These data indicate that the maximum representation of alkaliphilous taxa in all the samples analysed from core 2, was no greater than 4.5 *per cent* of the total count per sample. In contrast, the representation of acidophilous taxa exhibit a wider range of values, attaining a maximum 25.4 *per cent* of the total count per sample.

Table 46 - The proportion of different pH categories of fossil diatoms represented in Core 2

Depth in	Acp		Ind		Alp		Unknown		No. of taxa	
Core 2 (cm)	No	%	No	%	No	%	No	%	Types	Σ
0.5	29.5	5.9	459.5	91.9	6	1.2	5	1.0	25	500
6.0	80.5	16.1	387	77.4	10.5	2.1	21	4.2	49	499
11.0	83	16.6	396.5	79.3	9.5	1.9	12	2.4	39	501
20.0	71	14.2	419	83.8	9	1.8	1	0.2	25	500
26.5	127	25.4	353.5	70.7	10	2.0	9.5	1.9	42	500
34.0	87	17.4	380.5	76.1	22.5	4.5	10	2.0	45	500
39.5	56.5	11.3	421	84.2	14	2.8	8.5	1.7	35	500
46.5	20.5	4.1	461	92.2	17.5	3.5	1	0.2	26	500
48.0	41.5	8.3	427	85.4	21	4.2	10.5	2.1	41	500
49.0	18.5	3.7	462.5	92.5	16.5	3.3	2.5	0.5	29	500
53.5	8	1.6	481	96.2	9	1.8	3	0.6	17	501

Table 47 - Count data for the seven dominant alkaliphilous diatom taxa represented in core 2

	Depth in core 2 (cm)										
Taxon	0.5	6.0	11.0	20.0	26.5	34.0	39.5	46.5	48.0	49.0	53.5
Cymbella microcephala		2			1	7	2	1			
Synedra acus var. *radians*		1				3	1	5	2		
Fragilaria construens									5	4	2
Fragilaria vaucheriae	3			2					2		
Fragilaria construens var. *binodis*						2		2	2		
Gomphonema gracile		4	1		2	1	1	1		1	
Diatoma elongatum							7				
Total numerical count of these seven taxa per sample	3	7	1	2	3	13	11	9	11	5	2
Total count of all alkaliphilous taxa expressed as a percentage	1.2	2.1	1.9	1.8	2.0	4.5	2.8	3.5	4.2	3.3	1.8

Table 48 - Count data for the seven dominant acidophilous diatom taxa represented in core 2

	Depth in core 2 (cm)										
Taxon	0.5	6.0	11.0	20.0	26.5	34.0	39.5	46.5	48.0	49.0	53.5
Melosira distans var. *alpigena*	13	29	38	42	83	43	42	8	13	5	7
Anomoeoneis serians var. *brachysira*	10	22	20	21	23	19	5	9	21	10	
Tabellaria fenestrata		10	8	2	5	4	1		3	1	
Frustulia rhomboides var. *saxonica*		6	7	2	5	4	3		1		
Eunotia tenella		7		2	1	3	3			1	
Eunotia pectinalis var. *minor*	4			1	1	4			1		
Navicula cocconeiformis		2	1		1	1				1	
Total numerical count of these seven taxa per sample	27	76	74	70	119	78	53	17	39	18	7
Total count of all acidophilous taxa expressed as a percentage	5.9	16.1	16.6	14.2	25.4	17.4	11.3	4.1	8.3	3.7	1.6

The dominant alkaliphilous diatom taxa represented in the samples analysed from sediment core 2, were in descending order of abundance as follows: *Cymbella microcephala, Synedra acus* var. *radians, Fragilaria construens, F. vaucheriae, F. construens* var. *binodis, Gomphonema gracile* and *Diatoma elongatum.* The count data for the seven dominant alkaliphilous diatom taxa represented in core 2 are presented in Table 47.

The dominant acidophilous diatom taxa represented in the samples analysed from core 2 were in descending order of abundance as follows: *Melosira distans* var. *alpigena, Anomoeoneis serians* var. *brachysira, Tabellaria fenestrata, Frustulia rhomboides* var. *saxonica, Eunotia tenella, E. pectinalis* var. *minor* and *Navicula cocconeiformis.* The count data for the seven dominant acidophilous diatom taxa represented in core 2 are presented in Table 48.

The pH indifferent (circum-neutral) diatom taxa comprised the largest category in all the samples analysed from core 2. Furthermore, this pH category was dominated by species of the genus *Cyclotella.*

The proportion of different salinity (halobion) tolerance categories of fossil diatoms in core 2 are indicated in Table 49. These data indicate that the maximum representation of halophilous taxa in all the samples analysed from core 2 was no greater than 1.4 *per cent* of the total count per sample. Indeed, in several cases no halophilous taxa were recorded per counted sample. The diatom taxa defined as halophilous comprised the following three taxa: *Diatoma elongatum, Nitzschia frustulum* and *Stauroneis prominula.* In contrast, the representation of halophobous taxa exhibited a wider range of values, attaining a maximum 14.8 *per cent* of the total count per sample. The dominant halophobous diatom taxa represented in the samples analysed from core 2, were in descending order of abundance as follows: *Anomoeoneis serians* var. *brachysira, Fragilaria virescens, Tabellaria fenestrata, Frustulia rhomboides* var. *saxonica, Eunotia tenella, E. pectinalis* var. *minor* and *E. arcus.* The count data for the seven dominant halophobous diatom taxa represented in core 2 are presented in Table 50. The diatom taxa *Anomoeoneis serians* var. *brachysira, Tabellaria fenestrata, Frustulia rhomboides* var. *saxonica, Eunotia tenella* and *E. pectinalis* var. *minor* also exhibit acidophilous affinities.

Table 49 - The proportion of different salinity tolerance categories of fossil diatoms represented in Core 2

Depth in	Hp		Ind		Hb		Unknown		No. of taxa	
Core 2 (cm)	No	%	No	%	No	%	No	%	Types	Σ
0.5	0	0.0	478	95.6	17	3.4	5	1.0	25	500
6.0	0	0.0	410	82.0	74	14.8	15	3.0	49	499
11.0	0	0.0	439	87.8	53	10.6	9	1.8	39	501
20.0	0	0.0	467	93.4	31	6.2	2	0.4	25	500
26.5	2	0.4	440.5	88.1	49.5	9.9	8	1.6	4.2	500
34.0	0	0.0	443	88.6	48	9.6	9	1.8	45	500
39.5	7	1.4	461	92.2	25	5.0	7	1.4	35	500
46.5	0	0.0	483	96.6	16	3.2	1	0.2	26	500
48.0	2	0.4	458	91.6	31	6.2	9	1.8	41	500
49.0	0	0.0	478	95.6	20	4.0	2	0.4	29	500
53.5	0	0.0	487	97.4	11	2.2	3	0.6	17	501

Table 50 - Count data for the seven dominant halophobous diatom taxa represented in core 2

	Depth in core 2 (cm)										
Taxon	0.5	6.0	11.0	20.0	26.5	34.0	39.5	46.5	48.0	49.0	53.5
Anomoeoneis serians var. *brachysira*	10	22	20	21	23	19	5	9	21	10	
Fragilaria virescens	2	17	9	2	5	5	8	3	3	5	10
Tabellaria fenestrata		10	8	2	5	4	1		3	1	
Frustulia rhomboides var. *saxonica*		6	7	2	5	4	3		1		
Eunotia tenella		7		2	1	3	2			1	
Eunotia pectinalis var. *minor*	4			1	1	4			1		
Eunotia arcus		3				3	2		1		
Total numerical count of these seven taxa per sample	16	65	44	30	40	42	21	12	30	17	10
Total count of all halophobous taxa expressed as a percentage	3.4	14.8	10.6	6.2	9.9	9.6	5.0	3.2	6.2	4.0	2.2

VARIATION IN THE REPRESENTATION OF ACIDOPHILOUS DIATOM TAXA IN THE FOSSIL RECORD FROM LOCH MORAR

Data relating to the various ecological categories represented by the fossil diatom taxa are indicative of changes in ecological preferences of the diatom assemblages, which may correlate with changes in the lithostratigraphic succession and the fossil pollen record of the sediments.

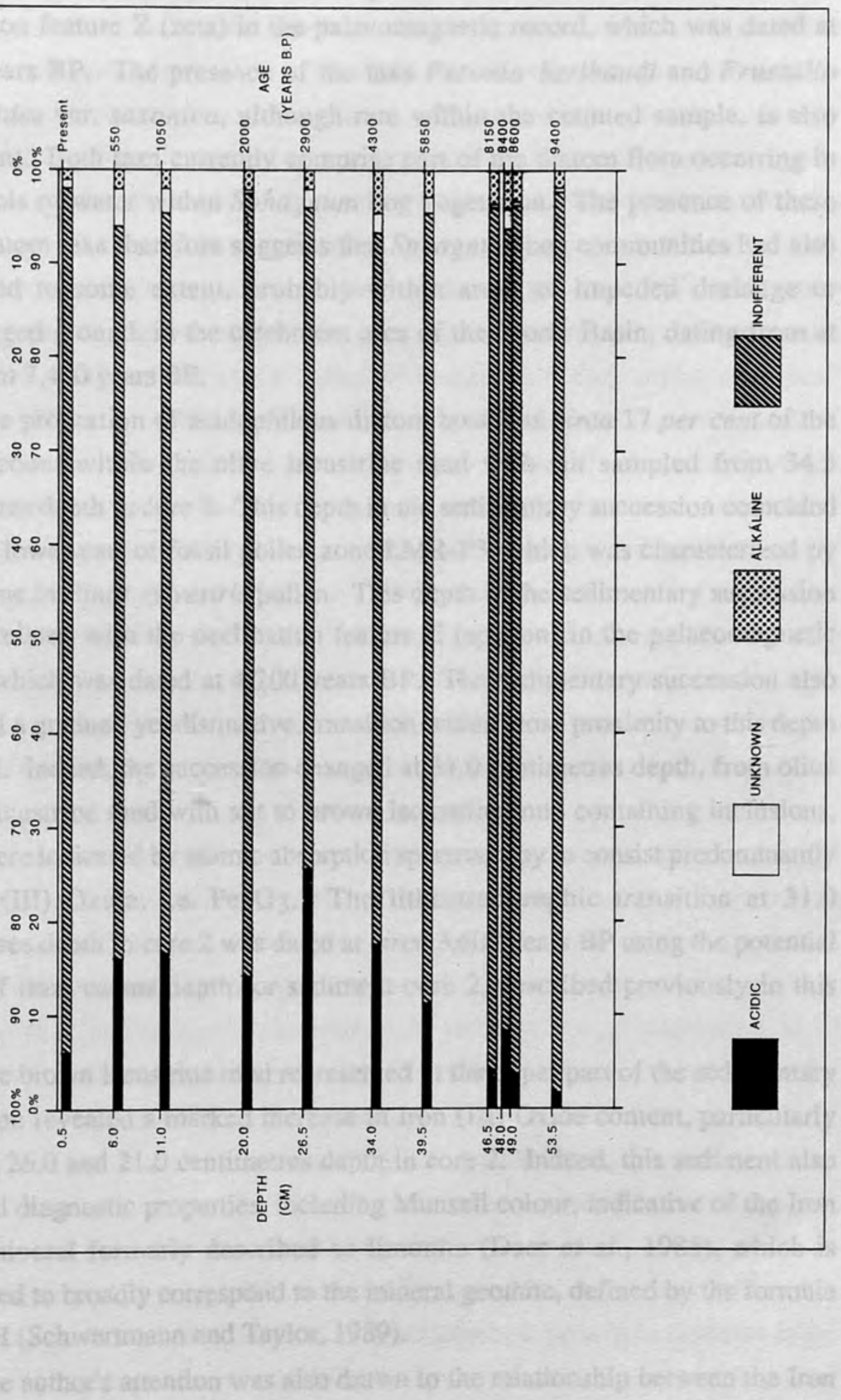
Data relating to the proportion of taxa corresponding to the different pH categories represented in the fossil diatom record from Loch Morar are illustrated in Figure 23. These data indicate that the proportion of acidophilous diatoms per sample count ranges between 1.6 and 25.4 *per cent* among the fossil samples analysed. This suggests that significant changes in water pH have occurred in the catchment area of the Morar Basin during the period represented by the fossil diatom record.

Among the range of acidophilous taxa recorded from the sedimentary succession were taxa belonging to the genus *Eunotia*. Significantly, *E. monodon, E. pectinalis, E. pectinalis* var. *minor* and *E. tenella* were recorded from the lowermost samples analysed, i.e. from 49.0 centimetres depth in core 2. Although these taxa were generally rare within the lower part of the fossiliferous sediments, their presence is nevertheless significant. *Eunotia* species are currently associated with acidic moorland vegetation (Round, 1957).

Additional indicators of acidic environments were also recorded in samples analysed above 48.0 centimetres depth in core 2. These indicators included the taxa *Melosira distans* var. *alpigena, Pinnularia undulata, Peronia heribaudi, Frustulia rhomboides* and *F. rhomboides* var. *saxonica.* The sediment sampled from 48.0 centimetres depth in core 2 corresponds with the base of the olive lacustrine mud with silt in the sedimentary succession. Furthermore, there was also an increase in organic carbon content of the sedimentary succession from this depth upward in core 2, which possibly reflects increasing biological productivity in the limnological environment, and soil maturation within the catchment area of the Morar Basin. Indeed, this depth in the sedimentary succession coincided with the lower part of fossil pollen zone LMR-P1, which was characterized by the appearance and subsequent increase in *Pinus sylvestris* pollen. This depth in the sedimentary succession also correlated with the declination feature H (eta) in the palaeomagnetic record, which is dated at 7,400 years BP. The fossil diatom record therefore suggests that acidic moorland vegetation had begun to develop to some extent, probably within a mosaic of other plant communities, in the catchment area of the Morar Basin during the early part of the Holocene Epoch.

While the proportion of acidophilous diatom taxa is generally less than 10 *per cent* of the sample count in the oldest part of the fossil record, these data

Fig.23 PROFILE OF pH SPECTRA OF FOSSIL DIATOMS FROM LOCH MORAR SEDIMENT CORE 2



indicate a general increase in the proportion of the acidophilous planktonic taxon *Melosira distans* var. *alpigena* within the olive lacustrine mud with silt sampled from 39.5 centimetres depth in core 2. Indeed, this depth in the sedimentary succession coincided with the lower part of fossil pollen LMR-P2, which was characterized by the appearance and subsequent increase in *Alnus glutinosa* pollen. This depth in the sedimentary succession also correlated with the declination feature Z (zeta) in the palaeomagnetic record, which was dated at 6,300 years BP. The presence of the taxa *Peronia heribaudi* and *Frustulia rhomboides* var. *saxonica*, although rare within the counted sample, is also significant. Both taxa currently comprise part of the diatom flora occurring in open pools of water within *Sphagnum* bog vegetation. The presence of these fossil diatom taxa therefore suggests that *Sphagnum* bog communities had also developed to some extent, probably within areas of impeded drainage or waterlogged ground, in the catchment area of the Morar Basin, dating from at least *circa* 7,400 years BP.

The proportion of acidophilous diatom taxa was *circa* 17 *per cent* of the sample count within the olive lacustrine mud with silt sampled from 34.5 centimetres depth in core 2. This depth in the sedimentary succession coincided with the lower part of fossil pollen zone LMR-P3, which was characterized by the decline in *Pinus sylvestris* pollen. This depth in the sedimentary succession also correlated with the declination feature E (epsilon) in the palaeomagnetic record, which was dated at 4,200 years BP. The sedimentary succession also exhibited a gradual, yet distinctive, transition within close proximity to this depth in core 2. Indeed, the succession changed at 31.0 centimetres depth, from olive brown lacustrine mud with silt to brown lacustrine mud containing inclusions, which were indicated by atomic absorption spectroscopy to consist predominantly of Iron (III) Oxide, i.e. Fe_2O_3. The lithostratigraphic transition at 31.0 centimetres depth in core 2 was dated at *circa* 3,600 years BP using the potential model of time versus depth for sediment core 2, described previously in this chapter.

The brown lacustrine mud represented in the upper part of the sedimentary succession revealed a marked increase in Iron (III) Oxide content, particularly between 26.0 and 21.0 centimetres depth in core 2. Indeed, this sediment also exhibited diagnostic properties, including Munsell colour, indicative of the Iron Oxide mineral formerly described as limonite (Deer *et al.*, 1985), which is considered to broadly correspond to the mineral geothite, defined by the formula $\alpha FeOOH$ (Schwertmann and Taylor, 1989).

The author's attention was also drawn to the relationship between the Iron Oxide-enriched lacustrine mud and the fossil diatom record from core 2. Indeed, among the fossil samples analysed from core 2, the proportion of acidophilous diatom taxa comprised *circa* 25 *per cent* of the sample count, within brown lacustrine mud sampled from 26.5 centimetres depth. This represented the highest value recorded for this category of diatoms in the fossil record from Loch Morar.

Among the acidophilous diatom taxa represented in this sample the planktonic diatom *Melosira distans* var. *alpigena* was particularly significant because it comprised *circa* 17 *per cent* of the sample count, which represented its maximum value recorded among the fossil samples analysed. Indeed, this taxon represented the second most abundant diatom in this sample, succeeding the planktonic species of the genus *Cyclotella,* which comprised the dominant taxa throughout the fossil diatom record from Loch Morar.

Other acidophilous taxa represented in the sample from 26.5 centimetres depth included *Anomoeoneis serians* var. *brachysira* (which attained its maximum recorded representation, along with *Anomoeoneis exilis*, among the fossil samples analysed), *Tabellaria fenestrata, Frustulia rhomboides* var. *saxonica, Cymbella perpusilla, Eunotia pectinalis* var. *minor, E. tenella, Navicula cocconeiformis*, and *Peronia heribaudi*, in descending order of abundance. The taxon *Cymbella perpusilla* is notable because it currently exhibits acidobiontic affinities.

The sample taken from 26.5 centimetres depth was dated at *circa* 2,900 years BP using the potential model of time versus depth for sediment core 2, while the adjacent lithostratigraphic transition to brown lacustrine mud enriched with Iron (III) Oxide at *circa* 26.0 centimetres depth was dated at *circa* 2,800 years BP.

The proportion of acidophilous diatom taxa generally comprised *circa* 15 *per cent* sample count in the majority of the fossil samples taken from brown lacustrine mud represented in the uppermost part of the sedimentary succession, i.e. between 20.0 centimetres depth and the inferred sediment-water interface at the top of core 2. The base of this part of the sedimentary succession, i.e. at 20 centimetres depth, correlated with the declination feature Γ (gamma) in the palaeomagnetic record, which was dated at 2,000 years BP. The upper part of the sedimentary succession, corresponding with the top of core 2, was interpreted as representing the product of recent sediment deposition on the basis of magnetic inclination data presented previously in this chapter.

A fossil diatom sample taken from 0.5 centimetres depth in core 2, within close proximity to the inferred sediment-water interface, revealed a decrease in the proportion of acidophilous diatom taxa to *circa* 6 *per cent* of the sample count. This contrasted with values of *circa* 15 *per cent* which were recorded in the remainder of the fossil samples taken from the brown lacustrine mud represented in the uppermost part of the sedimentary succession, i.e. the upper 20 centimetres of sediment core 2.

Thus, to summarize the principal findings of the fossil diatom analysis, it is evident from the ecological spectra of the fossil diatom taxa represented in the fossil record that Loch Morar was oligotrophic in status *sensu* Hustedt (1937-39) during the Holocene Epoch. Planktonic diatoms of the genus *Cyclotella* comprised the dominant taxa in the fossil record. The predominant pH category represented in the fossil record comprised the pH indifferent (circum-neutral) category, followed in decreasing order of overall abundance by the acidophilous and alkaliphilous categories, respectively. Although the alkaliphilous diatom taxa generally comprised a minor component in the pH spectra of the fossil record, samples dating from the early part of the Holocene Epoch, nevertheless, revealed the presence of several *Fragilaria* species, including *F. construens* and *F. contruens* var. *venter*, which were also prominent among the pioneer diatom flora recorded on the volcanic island of Surtsey, Iceland, and were among the first diatom taxa to appear in many Late Devensian Lateglacial diatom assemblages in the British Isles.

The acidophilous diatom taxa represented in the fossil record from Loch Morar included representatives of the genus *Eunotia*, in particular *E. monodon, E. pectinalis* and *E. tenella*, which were represented in samples dated to at least *circa* 7,400 years BP, contemporaneous with an increase in fossil pollen of *Pinus sylvestris*. The presence of these diatom taxa, which are currently associated with acidic moorland vegetation, although generally rare within the older part of the fossil record, suggest that acidic moorland vegetation had probably developed to some extent in the catchment area of the Morar Basin, at least by *circa* 7,400 years BP. Furthermore, the presence of other acidophilous taxa, in particular *Frustulia rhomboides* var. *saxonica* and *Peronia heribaudi*, which are distinctive components of the current diatom flora typically associated with open water pools in *Sphagnum* bog communities, suggests that bog vegetation had also developed to some extent, probably on waterlogged ground in the catchment area of the Morar Basin, dating from at least this time. The proportion of acidophilous diatom taxa represented in sediment dating from this period was between *circa* 4 and 8 *per cent* per sample count. A general increase in the proportion of acidophilous taxa evidently occurred thereafter, attaining a value of *circa* 17 *per cent* per sample count in a sample dated at *circa* 4,200 years BP, which also corresponded with a marked decrease in *Pinus sylvestris* pollen in the fossil pollen record. The maximum representation of acidophilous diatom taxa in the fossil record, attaining a value of *circa* 25 *per cent* per sample count, was recorded in a fossil sample dated at *circa* 2,900 years BP. This sample also correlated with a contemporaneous increase in Iron (III) Oxide content in the sedimentary succession. A subsequent general decrease in the representation of acidophilous diatom taxa, to *circa* 15 *per cent* per sample count, was recorded in fossil samples dated to post 2,000 years BP, while a value of only *circa* 6 *per cent* per sample was recorded in a sample taken within close proximity to the sediment-water interface of the sedimentary succession from Loch Morar.

THE SIGNIFICANCE OF IRON OXIDES IN THE SEDIMENTARY SUCCESSION FROM LOCH MORAR

The increase in Iron (III) Oxide, i.e. Fe_2O_3, in the sedimentary succession from Loch Morar may be attributed to a variety of processes. However, evidence from the fossil diatom record appears to suggest at least one possible process involving *Sphagnum* bog vegetation in the catchment area. The significance of Iron (III) Oxide in the sedimentary succession was inferred from a consideration of the chemistry of the Iron-cycle, which is briefly described below.

Iron forms a principal constituent of the Earth's lithosphere, occurring in most rocks which form the planet's crust. The element Iron (symbol Fe), which is included among the Transition Elements in the Periodic Table of Elements, exhibits a complex chemistry, in particular, it may form positively charged ions, (i.e. cations), of different individual oxidation states (Fe^{2+} and Fe^{3+}, respectively), whose solubility is dependent upon redox potential and pH. Thus, Fe^{2+} is more soluble than Fe^{3+} at an equivalent pH.

In most magmatic rocks, Iron is predominantly bound within silicates in its divalent oxidation state, i.e. as Fe^{2+} cations. The release of Iron from silicates in rock may arise during weathering by means of the chemical processes of protolysis and oxidation. Thus, hydrogen protons (H^+) arising from the solution of CO_2 in water, may break down silicate-bearing minerals to release Fe^{2+} cations. The liberated Fe^{2+} cations may then be readily oxidized to Fe^{3+} cations in aerobic conditions (Schwertmann and Taylor, 1989). Alternatively, oxidation may also occur within the silicate-bearing minerals (Berner and Schott, 1982). Indeed, Iron exhibits a strong tendency to hydrolyze and form oxides with relatively low solubilities, because the cation has a high affinity for the hydroxyl (OH^-) ligand, thus making the hydrated Fe^{3+} cation a strong acid. Furthermore, it also readily polymerizes as hydrolysis proceeds. The resulting Iron (III) Oxide may be easily re-mobilized as a result of chemical reduction, particularly under anaerobic conditions, e.g. in waterlogged soils. The divalent Fe^{2+} cation thus formed may be either re-mobilized *in situ* or translocated and oxidized to Fe^{3+} in a new environment, e.g. within oxygenated water, therefore giving rise to new mineral phases. Thus, Iron Oxides may undergo variable periods of immobilization and mobilization, which may be cyclic over quite short periods of time (Schwertmann and Taylor, 1989).

The principal forms of Iron in aqueous solution include inorganic Fe^{2+} and Fe^{3+} cations respectively, and soluble organic complexes of these cations bonded as ligands. These forms may originate from any solid Iron compounds, including primary Iron-silicates, Iron (II) Carbonate, i.e. $FeCO_3$, Iron (II) and Iron (III) hydroxy compounds, i.e. $Fe(OH)_2$ and $Fe(OH)_3$ respectively, and also from Iron (III) Oxides, which may be transformed into other Iron Oxides after their dissolution (Schwertmann and Taylor, 1989). Iron, once precipitated as sparingly soluble Iron (III) Oxide may be re-mobilized by chemical reduction. This process typically occurs when dissolved Oxygen becomes deficient, e.g. in poorly drained soils. Indeed, many micro-organisms, particularly anaerobic bacteria, are capable of reducing Iron Oxides; microbiological reduction of Iron Oxides is probably the most important process involved in the Iron-cycle in soils (Ottow and Glathe, 1971; Schwertmann *et al.*, 1985). The resultant Fe^{2+} cations dissolve in aqueous solution, and subsequently undergo oxidation to form Iron Oxides, either during re-mobilization, or *in situ,* when aerobic conditions are restored. Oxidation may occur by direct chemical reaction with dissolved Oxygen, or as a result of biochemical processes, particularly involving micro-organisms, notably bacteria of the Chlamydobacteriales (Lundgren and Dean, 1979). Indeed, some taxa of bacteria, e.g. *Thiobacillus ferrooxidans,* are adapted to strongly acidic conditions, often where the $pH<3.0$, wherein they can oxidize Fe^{2+} cations in aqueous solution; under these circumstances abiotic oxidation of Fe^{2+} cations proceeds only extremely slowly. The activity of this bacterium is particularly significant in relation to water enriched with Iron cations which has passed through strongly acidic soil (Crerar *et al.*, 1979). The biotic formation of Iron Oxides may also arise from the metabolic oxidation of organic complexes of Iron cations bonded as ligands. This process is achieved by a large variety of heterotrophic micro-organisms, and it results in the immediate release of Fe^{2+} cations, which subsequently undergo hydrolysis and precipitation (Schwertmann and Taylor, 1979).

Significantly, water within pools and streams in *Sphagnum* bog vegetation is acidic, typically ranging between pH 3.0-5.0. Therefore, on the basis of the chemistry of the Iron-cycle indicated above, it is reasonable to suggest that acidic ground-water draining *Sphagnum* bog vegetation could transport Iron in aqueous solution, typically in a reduced oxidation state as Fe^{2+} cations, which would subsequently undergo oxidization under appropriate chemical conditions to form

Fe_2O_3 at any point *en route* to its eventual incorporation within the sedimentary succession in Loch Morar.

Iron undoubtedly exists in the catchment area of the Morar Basin in a variety of forms. Indeed, the sedimentary succession from Loch Morar exhibits a distinctive textural change which coincided with the Fe_2O_3 enrichment of the succession. This change in sediment texture is interpreted by the author as possibly representing the incorporation of colloidal complexes of Iron, humus and silicates within the sediment matrix. Furthermore, this change also corresponded with an observed aggregation of fossil diatom frustules, in prepared fossil samples from Loch Morar. This phenomenon has also been reported from other lacustrine sites in northern Scotland (Pennington *et al.*, 1972) where it has been directly attributed to the presence of colloidal complexes of Iron within the lacustrine sediments.

THE POSSIBLE SIGNIFICANCE OF *SPHAGNUM* BOG DEVELOPMENT IN RELATION TO THE HISTORY OF NATIVE FOREST COVER OF THE MORAR BASIN

The development and expansion of *Sphagnum* bog communities in Morar Basin, indicated in the fossil record from Loch Morar, may have significant implications in relation to the native forest cover of this area during the Holocene Epoch.

Various factors may have operated both singly and together which could account for the increase in *Sphagnum* bog vegetation in the catchment area. In particular, climatic conditions, soil maturation and anthropogenic activity may have been amongst the most significant (Moore, 1975). Furthermore, these factors probably also affected and influenced the spatial distribution and floristic composition of the forest cover of the Morar Basin. Palaeoecological data which support this hypothesis are reviewed below.

The fossil records from many sites in the British Isles indicate that anthropogenic activities involving the burning, felling and clearance of woodland cover have progressively affected the floristic composition of the vegetation cover and the landscape in many regions of the British Isles, during the last 5,000 years (Birks, H.J.B., 1977), with an overall tendency towards deforestation, which corresponds with cultural evolution from the Neolithic to the modern age. In particular, fossil data suggest that by *circa* 2,000 years BP, large areas of the Scottish landscape were essentially treeless (Walker, 1984).

Tree felling and forest clearance are often indicated in the fossil record in a variety of forms, including a relative increase in the mineral particle contribution to the sedimentary succession, which is generally discernible from changes in the sediment lithology coupled with relative increases in natural remanent magnetic intensity and susceptibility. In addition, distinctive fossil biota including the soil-dwelling diatom *Hantzschia amphioxys*, and an increase in open habitat taxa, e.g. Gramineae, Ericaceae (particularly *Calluna vulgaris*) and *Pteridium aquilinum*, accompanied by flora typically associated with arable and pastoral cultivation, including representatives of the Compositae, Chenopodiaceae and Caryophyllaceae, *Artemissia* spp., *Rumex* spp., *Plantago lanceolata* and cereals of *Triticum* spp. and *Hordeum* spp. etc., are also strongly indicative of anthropogenic activity in the landscape (Walker, 1984).

Episodes of former forest clearance during the Holocene Epoch often correlate with broadly contemporaneous increases in the rate of sedimentation within lacustrine sites, e.g. in the Cumbrian lakes, north-west England (Pennington, 1964, 1970). In many cases, extensive forest clearance was succeeded by the development of grassland and dwarf-shrub heath communities and the initiation of *Sphagnum* bog development, e.g. in the Welsh uplands (Moore, 1973), Exmoor (Moore, 1974), and the Sperrin Mountains, Northern Ireland (Smith, 1975). The action of fire on vegetation, whether arising from anthropogenic activity or from lightning strikes, is also indicated in the fossil record by the presence of distinctive particles of charcoal, which are often represented as horizons within peat and soil profiles (Durno and McVean, 1959; McVean, 1964b), and by the presence of carbonized fragments in lacustrine sediment profiles (Birks, H.H., 1972a).

Although anthropogenic activity is widely indicated as one of the primary causes of deforestation during the Holocene Epoch in many districts of the Scottish Highlands, e.g. the Galloway Hills, south-west Scotland (Birks, H.H., 1972b) and the eastern Grampian Highlands (Huntley, 1981), there is nevertheless, reasonable evidence to suggest that climatic factors may have been involved in some areas, e.g. Loch Maree, north-west Scotland (Birks, H.H., 1972b) and northern Scotland (Pennington *et al.*, 1972). Climatic conditions probably exerted a significant influence on the vegetation cover in remote north-west Highland areas, particularly where anthropogenic occupation was relatively sparse.

The fossil record from Loch Maree, in Ross-shire, NW Scotland, suggests that during the Holocene Epoch, deforestation in this area occurred primarily by natural means, perhaps due to climatic changes, rather than by burning, felling or grazing (Birks, H.H., 1972a). In particular, fossil pollen of *Pinus sylvestris* and *Quercus* spp. decreased markedly in lacustrine sediments radiocarbon-dated to 4,206±55 years BP (Q-1005), to be replaced by pollen of dwarf-shrub and bog communities. The decline in the local woodland and its replacement by bog and heath are attributed to a relative increase in the oceanicity of the prevailing climate; anthropogenic factors are considered unlikely to have been contributory as there is little archaeological evidence for contemporary occupation (Birks, H.H., 1972a). Buried horizons of fossil *Pinus sylvestris* tree stumps in coastal peat beds farther northward at Badentarbert, near Achiltibuie, Ross-shire, have been radiocarbon dated to between 4,420±102 years BP (NPL-13) and 4,220±105 years BP (NPL-14). The decline of this particular Scots pine forest has been attributed to climatic deterioration (Lamb, 1964). Independent evidence from the chemical analysis of lacustrine sediment profiles from northern Scotland (Pennington *et al.*, 1972) and stratigraphic studies of Scottish blanket peats containing macro-fossil remains of *Pinus sylvestris* (Birks, H.H., 1975) indicate a change to a more oceanic climate with strong winds, increased precipitation and cloudiness at this time (Birks, H.J.B., 1977).

A recent study of the history and palaeoclimatic significance of sub-fossil remains of *Pinus sylvestris* in blanket peats from Scotland (Bridge *et al.*, 1990) indicates that the density and distribution of this taxon varied significantly within Scotland during the Holocene Epoch, probably as a result of variations in precipitation levels. Indeed, stable isotope variation data indicate particularly wet conditions at *circa* 7,500, 6,250-5,800, 4,250-3,870 and 3,300 years BP, respectively. Furthermore, a time-lag between climatic change and subsequent reduction in *Pinus sylvestris* is also indicated (Bridge *et al.*, 1990). These climatic conditions would therefore inhibit the regeneration of *Pinus sylvestris* on mineral soils, by reducing the number of good seed years, and also promote increased soil podsolization and soil deterioration. Furthermore, as a direct consequence of a pronounced oceanic climate regime, an increase in the ratio of precipitation to evaporation would cause waterlogging to become more widespread, and hence encourage the expansion of blanket bog vegetation (Birks, H.J.B., 1977).

The growth of *Sphagnum* mosses in shallow basins and pools of water on terrain which is habitually waterlogged, may be followed under certain circumstances by the development of *Sphagnum* bog communities. The development of a *Sphagnum* bog is generally dependent upon conditions of high rainfall incidence and low evaporation and transpiration. Under these climatic conditions, and upon impervious acidic rock substrata, blanket bog may develop on most terrain apart from the steepest slopes and well drained ground. Furthermore, during the course of geological history the gradual accumulation of partially decomposed or undecomposed bog vegetation may result in the formation of massive unconsolidated deposits of peat; within the Morar Basin, blanket peat has accumulated to form deposits which are several metres deep in places, e.g. at Lochan a'Chleirich, described earlier in this chapter.

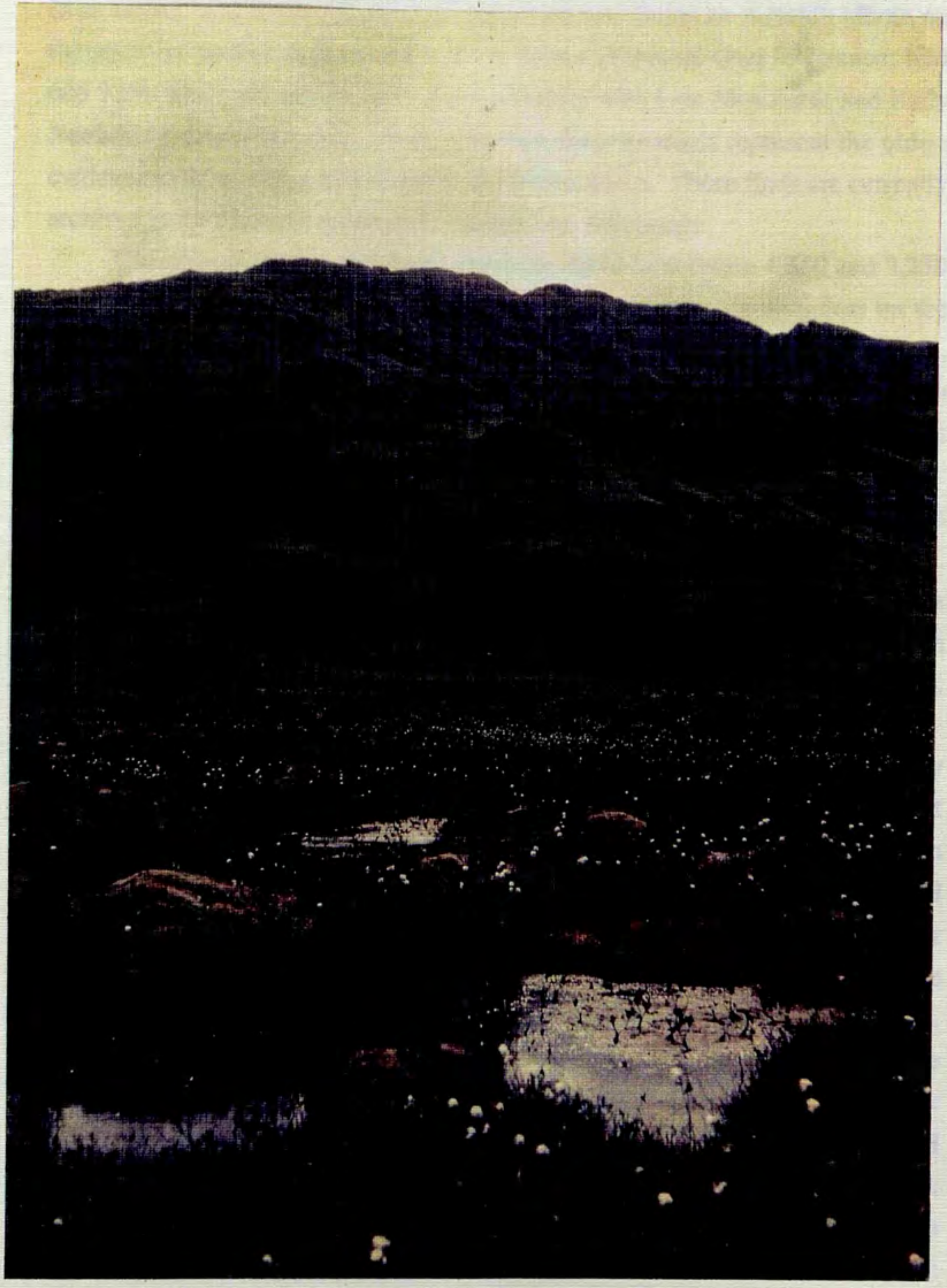
The reasons for the widespread and spectacular decline in *Pinus sylvestris* pollen at about 4,000 years BP in north-west Scotland, and the severe reduction of *Pinus sylvestris* throughout most of its geographical distribution range in the British Isles by this date (Bennett, 1984) are unclear, but a combination of climatic changes (Bennett, 1984) and anthropogenic activity, including burning, may have initiated the replacement of *Pinus sylvestris* communities on flat and gently sloping terrain by blanket bog vegetation (Birks, H.J.B., 1977), generally restricting these woodland communities to steep slopes and well drained terrain, which are unfavourable for blanket bog development.

A view of a well developed example of *Sphagnum* bog vegetation occurring in the western part of the Morar Basin is illustrated in Plate 12. The blanket bog of Mointeach Mhor, South Morar, exhibits floristic and ecological criteria which are characteristic of the *Trichophoreto-Eriophoretum typicum* (Western blanket bog) plant community *sensu* McVean and Ratcliffe (1962). This plant community contains the following constants: *Calluna vulgaris, Erica tetralix, Myrica gale, Eriophorum vaginatum, E. angustifolium, Molinia caerulea, Trichophorum caespitosum, Narthecium ossifragum, Drosera rotundifolia, Sphagnum papillosum, S. rubellum* and *H. cupressiforme.* On the wettest level-ground this association exhibits hummocks and pools where *Sphagnum* species often form a complete cover. The pools of water contain aquatic vascular plants including *Menyanthes trifoliata, Eriophorum angustifolium, Carex limosa, Sphagnum cuspidatum* and *S. papillosum* (Pearsall, 1956; Ratcliffe and Walker, 1958). The *Trichophoreto-Eriophoretum typicum* is one of the most widespread vegetation types in the Western Highlands of Scotland, on ground below *circa* 450 metres and on slopes of less than 10 degrees. This association occurs in many coastal areas of the extreme west of Scotland, often down to sea-level (McVean and Ratcliffe, 1962).

A combination of climatic factors and selective anthropogenic influence may therefore provide the strongest hypothesis to explain the variation in floristic composition and spatial distribution of indigenous tree cover in the Morar Basin during the Holocene Epoch.

The evidence of human occupation in this region of Scotland is briefly reviewed below.

Plate 12 Blanket bog at Mointeach Mhor, near Creag Mhor, South Morar



ARCHAEOLOGICAL EVIDENCE OF PREHISTORIC HUMAN OCCUPATION IN THE VICINITY OF THE MORAR BASIN

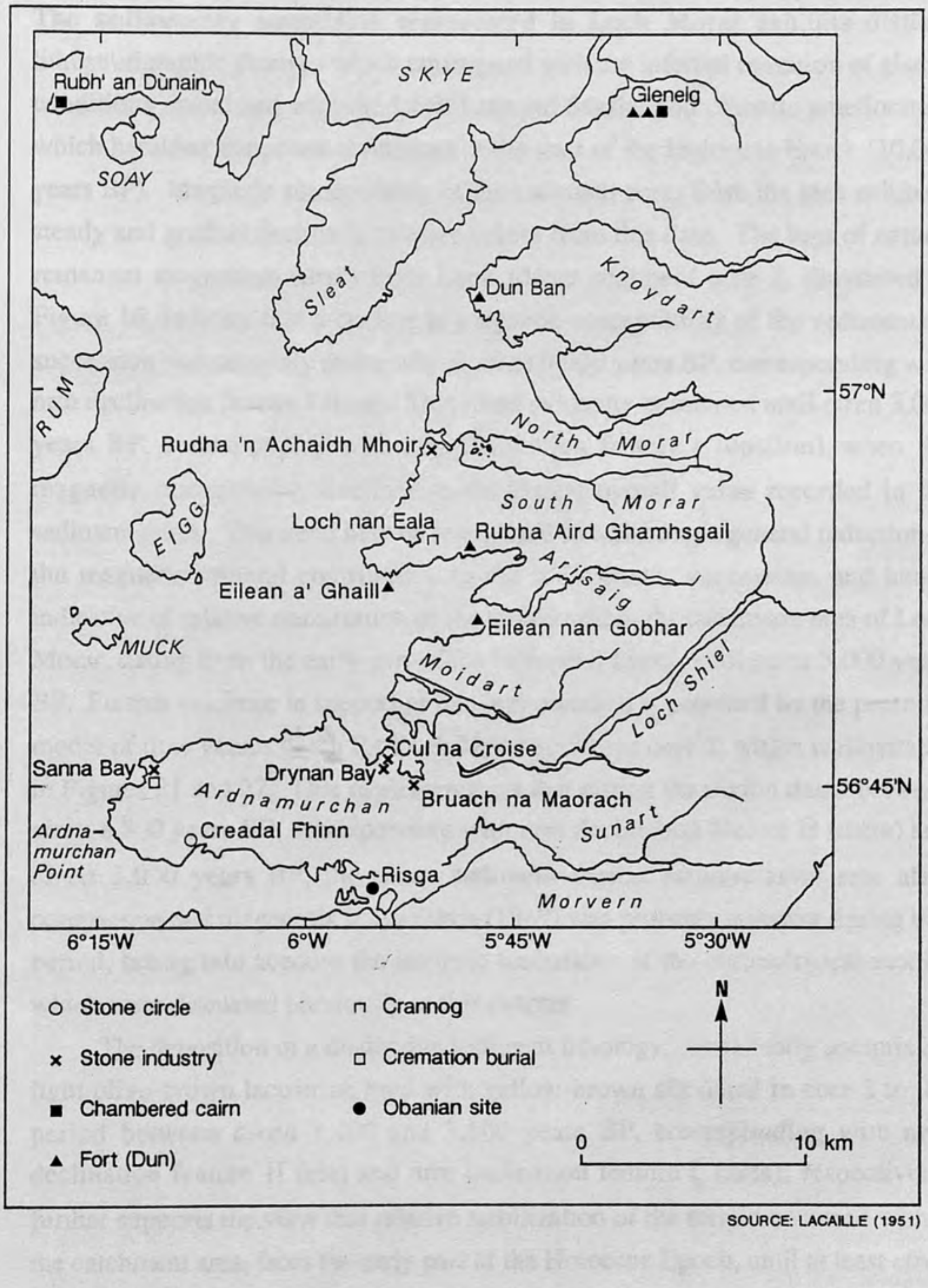
Archaeological evidence of human occupation in the Morar Basin is sparse. Prehistoric sites recorded in western Lochaber District (Lacaille, 1951) are indicated in Figure 24. A range of fashioned stone artefacts have been recorded from among sand dunes and machair vegetation near Beinn an Achaidh Mhoir, on the southern coastal margin of the River Morar (National Grid Reference: NM 666 925), which are attributed to share affinities with Late Mesolithic and Early Neolithic cultures (Lacaille, 1951). To date these artefacts represent the oldest evidence to date of human activity in the Morar Basin. These finds are currently archived at the National Museum of Antiquities, Edinburgh.

Chambered tombs and cairns generally dated to between 4,650 and 3,250 years BP, associated with Neolithic-Bronze Age cultures, are abundant on the nearby Isle of Skye (Daniell, 1962). A particularly fine tomb at Rubh'an Dùnain, near Loch Brittle (National Grid Reference: NG 393 164) has yielded human remains and Neolithic pottery (Clarke, 1933). These finds are also archived at the National Museum of Antiquities, Edinburgh.

Thus, it is possible that people of these cultures may have settled in the vicinity of Loch Morar, which is relatively near to the sites mentioned above. However, to date no direct evidence of such occupation in the Morar Basin has been recorded. Indeed, Neolithic and Bronze Age people probably lived in wooden homesteads, thatched with turf and heather (Renfrew, 1976; Grimble, 1980) that have not survived.

Impressive brochs, duns (hill-forts) and fortified homesteads, generally attributed to the Iron Age (*circa* 2,500 years BP) are represented on the Isle of Skye, e.g. on the Sleat Peninsula, and to the north of the Morar Basin in Knoydart district, e.g. Dun Telve and Dun Troddan, near Glenelg (National Grid References: NG 829 173 and NG 834 173, respectively) and Dun Ban, near Doune (National Grid Reference: NG 703 035). Dun Telve represents one of the finest surviving hill-forts in western mainland Scotland (Hawkes, 1986). Fortified homesteads are represented to the south of the Morar Basin, within the Sound of Arisaig, e.g. at Rubh' Aird Ghamshsgail (National Grid Reference: NM 694 840) and on the islands of Eilean a'Ghiall (National Grid Reference: NM 627 825) and Eilean nan Gobhar (National Grid Reference: NM 695 795). Although there are currently no radiocarbon dates from these sites, a semi-broch at Dun Ardtreck near Loch Harport, south-east Skye (National Grid Reference: NG 335 358) has been dated at 2,005±105 years BP (Mackie, 1969), which suggests that the duns in the Sleat Peninsula, south-eastern Skye, and those occurring on the adjacent mainland coast date from at least 2,000 years BP, and

Fig.24 PREHISTORIC SITES IN WESTERN LOCHABER AND SKYE



SOURCE: LACAILLE (1951)

possibly pre-date this archaeological feature on the basis of their design and construction (Birks and Williams, 1983).

EVIDENCE OF GENERAL STABILIZATION OF TERRAIN IN THE CATCHMENT AREA OF LOCH MORAR DURING THE HOLOCENE EPOCH AND ITS POSSIBLE IMPLICATIONS IN RELATION TO THE FOREST HISTORY

The sedimentary succession represented in Loch Morar exhibits distinct lithostratigraphic changes which correspond with the inferred cessation of glacial conditions associated with the Loch Lomond Stadial and climatic amelioration which heralded temperate conditions at the start of the Holocene Epoch (10,000 years BP). Magnetic susceptibility of the sediment cores from the loch exhibit a steady and gradual decline in relative values from this date. The logs of natural remanent magnetism (nrm) from Loch Morar sediment core 2, illustrated in Figure 16, indicate that a decline in magnetic susceptibility of the sedimentary succession was certainly under way at *circa* 9,900 years BP, corresponding with nrm declination feature I (iota). This trend evidently continued until *circa* 3,000 years BP, corresponding with nrm inclination feature ε (epsilon), when the magnetic susceptibility declined to its lowest overall value recorded in the sediment cores. This trend may be interpreted as reflecting a general reduction in the magnetic mineral contribution to the sedimentary succession, and hence indicative of relative stabilization of the terrain within the catchment area of Loch Morar, dating from the early part of the Holocene Epoch until *circa* 3,000 years BP. Further evidence in support of this interpretation is provided by the potential model of time versus depth for Loch Morar sediment core 2, which is illustrated in Figures 21 and 22. This model suggests that during the period dated between *circa* 8,800 years BP, corresponding with nrm declination feature Θ (theta) and *circa* 3,000 years BP, the mean sediment matrix accumulation rate after compaction and diagenesis *sensu* Davis (1969) was probably constant during this period, taking into account the intrinsic limitations of the chronological model, which were discussed previously in this chapter.

The deposition of a distinctive sediment lithology, consistently comprising light olive-brown lacustrine mud with yellow-brown silt dated in core 2 to the period between *circa* 7,400 and 3,600 years BP, corresponding with nrm declination feature H (eta) and nrm inclination feature ζ (zeta), respectively, further supports the view that relative stabilization of the terrain occurred within the catchment area, from the early part of the Holocene Epoch, until at least *circa* 3,600 years BP. Furthermore, no indicators of widespread clearance or burning of vegetation cover were identified within the sedimentary succession dating from this period.

From *circa* 3,000 years BP onwards, the logs of magnetic susceptibility and magnetic intensity exhibited a steady increase in magnitude. Shortly after *circa* 3,000 years BP, the lithostratigraphic succession also gradually changed from light olive-brown lacustrine mud with yellow-brown silt laminae, to dark brown lacustrine mud containing colloidal humic complexes with Iron (III) Oxide and silica.

Within the Holocene record, the logs of magnetic susceptibility and magnetic intensity both exhibit an overall zenith which corresponds with a distinctive layer of non-fossiliferous yellow silt. This sediment is dated at *circa* 2,000 years BP, corresponding with nrm declination feature Γ (gamma). Furthermore, the nrm intensity and susceptibility logs also revealed that this sediment exhibited values which were broadly similar in magnitude to the sediments deposited during the Loch Lomond Stadial. A possible interpretation is that this sediment may represent a re-distributed glacially-derived silt, which was transported to this site in the loch and incorporated within the sedimentary succession.

The period *post-circa* 2,000 years BP appears to have been characterized by a relative constancy in the supply of magnetic mineral particles, at least to the core sites in the loch. This is reflected in the logs of natural remanent magnetic intensity and magnetic susceptibility, which both exhibit a low order of magnitude and an almost constant trend throughout the period dated between *circa* 2,000 years BP to the present. The lithostratigraphic succession during this period is represented throughout by dark brown lacustrine mud, which exhibited an apparent time-depth dependent change in consolidation, i.e. the sediment matrix became less compacted and the water content increased within the sedimentary succession from *circa* 2,000 years BP to present. This trend is possibly reflected in the curvi-linear portion of the potential model of time versus depth for Loch Morar sediment core 2, illustrated in Figures 21 and 22.

The constant rate of sediment accumulation in Loch Morar, coupled with the absence of characteristic indicators of anthropogenic activity, within the sedimentary record embracing the greater part of the Holocene Epoch, at least between *circa* 8,800 years BP and *circa* 3,000 years BP, and perhaps shortly thereafter, supports the author's hypothesis that deforestation of the landscape within the Morar Basin, particularly around Loch Morar, occurred primarily by natural factors, perhaps including death by waterlogging, wind-throw, by lack of regeneration due to unfavourable edaphic conditions, and by the growth of blanket bog and moorland from *circa* 2,900 years BP, perhaps under increased oceanic climatic conditions. Anthropogenic activity, although undetected in the sedimentary succession and fossil record, may have been an additional factor, although, there is little evidence for subsequent anthropogenic interference in this area. However, the possibility exists that selective anthropogenic activity, e.g. localized forest clearances reflecting short periods of human occupation along with winter grazing by herbivorous livestock, as opposed to extensive clearances, may have initiated the degeneration of the tree cover, or accentuated its diminution, particularly during periods of deteriorating climatic conditions. Indeed, selective anthropogenic activity, perhaps dating from 4,000 years BP onwards, may have proved increasingly significant in relation to the history of the forest eco-system, and the processes which have resulted in the irregular distribution of the surviving native woodland cover of the Morar Basin.

Table 51 - Correlation of the lithostratigraphy, chronostratigraphy and biostratigraphy of the sedimentary succession in the profundal zone of Loch Morar

Depth in core 2 (cm)	Lithology	Palaeomagnetic secular variation	Inferred age (radiocarbon years BP)	Fossil pollen zone	Proportion of acidophilous fossil diatoms	Local developments
			Present		6%	*Quercus* and *Betula* from the dominant taxa in the native woodland cover with *Alnus* and *Salix* occurring on wetter soils
					16%	
10	Lacustrine mud					
					17%	
		B (θ_E)	1,200			
				LMR-P3		
20		Γ (θ_W)	2,000		14%	
	Silt					Lacustrine sediments rich in Fe_2O_3
	Limonite with lacustrine mud	Δ (θ_E)	2,500			
					25%	Highest % acidophilous diatoms
	Lacustrine mud	ε (θ_W)	3,000			
30						
		E (θ_E)	4,200	*Pinus* decline	17%	*Pinus sylvestris* decline at c.4,200 years BP
				LMR-P2		
40	Lacustrine mud with silt				11%	Increasing % acidophilous diatoms
		Z (θ_W)	6,300	*Alnus* increase		
				LMR-P1		
					4%	
	Silt	H (θ_E)	7,400	*Pinus* increase	8%	*Pinus sylvestris* appearance at c.7,400 years BP
50					4%	
		Θ (θ_E)	8,800			
					1%	
	Clay with silt and fine sand	I (θ_W)	9,900		Fossils rarely preserved in the sediments	Climatic amelioration associated with the start of Holocene period c.10,000 years BP
60						
70						
				No fossil pollen preserved in the sediments	No fossil diatoms preserved in the sediments	Deposition of laminated minerogenic sediments associated with glacial conditions of the Loch Lomond Stadial c.11,000 to 10,000 years BP
80						
	Laminated clay and fine sand					
90						

CHAPTER 6

SUMMARY OF THE PRINCIPAL FINDINGS

The mountain slopes and hill-sides surrounding Loch Morar, Highland Region, Scotland, currently support native broad-leaved deciduous woodland vegetation which occurs as discontinuous fragments of varying extent, while an archipelago of islands situated in Loch Morar supports stands of native coniferous woodland.

The woodland vegetation surrounding Loch Morar comprises several principal areas which individually cover *circa* 50 hectares, with smaller intermittent areas along both north and south shores of the loch. The broad-leaved deciduous woodland is referable to a combination of the *Betuletum Oxaleto-Vaccinetum (Vaccinium*-rich birchwood) and *Betula*-herb noda (herb-rich birchwood) *sensu* McVean and Ratcliffe (1962).

The woodland vegetation within the catchment area of the Morar Basin broadly corresponds with the zone of oak and birch forest *sensu* McVean and Ratcliffe (1962) which is considered to be representative of the predominant climax forest vegetation in western and south-western Scotland, prior to the Neolithic cultural period, *circa* 5,000 years BP.

A significant exception to this type of woodland cover is represented by stands of native coniferous woodland which occur on several islands near the western end of Loch Morar. This coniferous woodland vegetation, which collectively covers *circa* 21 hectares, is referable to a combination of the *Pinetum Hylocomieto-Vaccinetum* (Pinewood *Vaccinium*-moss) association and *Pinetum Vaccineto-Callunetum* (Pinewood *Vaccinium-Calluna*) association *sensu* McVean and Ratcliffe (1962).

The existence of native Scots pine, *Pinus sylvestris* var. *scotica*, on the Morar archipelago, situated at latitude 56°58'N by longitude 5°47'W indicates that the presumed geographical distribution range of this tree extends farther westwards in mainland Scotland, than the previously recorded western limit of 5°38'W at Shieldaig, Highland Region (Steven and Carlisle, 1959; Bennett, 1984).

The floristic composition and physiognomy of the broad-leaved deciduous woodland within the catchment area of the Morar Basin, and the coniferous woodland on the islands in Loch Morar, closely resemble native woodland vegetation described from other areas in the Scottish Highlands, while also exhibiting features that are indicative of ecological continuity of high tree cover as, opposed to coppice, over a long period.

A review of the epiphytic (corticolous) lichen flora of the woodland vegetation within the Morar Basin indicates that this area exhibits an outstanding range of lichen epiphytes, with many taxa that are currently restricted to the western regions of the British Isles, and often uniquely represented in coastal localities in western Scotland.

One outstanding area of oceanic broad-leaved deciduous woodland surrounds Lochan a'Chleirich, situated in hills beyond the western end of Loch Morar. This woodland supports over 110 different epiphytic lichen taxa, including at least 20 lichenological indicators of age and ecological continuity of high tree cover. These data strongly suggest that this site of broad-leaved woodland in particular, represents relict native Highland woodland, with ecological continuity of high tree cover, as distinct from coppice woodland. The coniferous Scots pine woodland occurring on the archipelago, in Loch Morar, is also floristically distinctive and exhibits a range of epiphytic lichen taxa that are characteristically associated with Boreal coniferous forest in Scotland. The floristic composition, physiognomy and presence of characteristic lichen epiphytes, strongly suggest that this coniferous woodland represents relic native Scots pine woodland, as opposed to a recent plantation of Scots pine.

Derivative plant communities, comprising *Calluna*-heath referable to the *Callunetum vulgaris* association *sensu* McVean and Ratcliffe (1962) along with acidic *Agrostis-Festuca* grassland referable to the species-poor *Agrosto-Festucetum* association *sensu* McVean and Ratcliffe (1962) have developed within the catchment area of the Morar Basin, upon ground which probably formerly supported native tree cover, while *Sphagnum* dominated bog is often highly developed upon ground which exhibits impeded drainage. Peat formation is widespread over areas of acid rocks in the prevailing oceanic climate.

The organic sediments which have accumulated in Loch Morar indicate that a number of significant events have occurred in the catchment area of the Morar Basin during the Holocene Epoch *sensu* Harland *et al.* (1989) *circa* 10,000 years BP to present.

Analysis of the palaeomagnetic secular variations recorded in long sediment cores obtained from the deep water zone in Loch Morar, provides a reliable method of establishing a chronology for the palaeoenvironment of the Morar Basin. The palaeomagnetic record, while significant in its own right, indicates a pattern of secular variation in magnetic declination, which is broadly comparable to the geomagnetic type curves for western Europe *sensu* Creer and Tucholka (1982a) covering the Holocene Epoch. These data are successfully integrated into a statistically significant model of time versus depth for the sedimentary succession in Loch Morar.

An outline analysis of fossil tree pollen preserved in the sedimentary record from Loch Morar, which was kindly supplied to the author, provides supplementary data relating to the history of the forest cover, and also provides independent chronological verification of the palaeomagnetic data. In particular, the appearance of fossil pollen of the tree *Alnus glutinosa*, is dated at *circa* 6500-6000 years BP, by comparison with published fossil pollen data from a nearby site at Lochan Doilead near Morar village (Williams, 1977; Birks, H.J.B., 1977). This event corresponds with magnetic declination feature Z (zeta) in the palaeomagnetic record, which is dated at *circa* 6300 years BP. Furthermore, fossil pollen of the tree *Pinus sylvestris* is also reported from Loch Morar, pre-dating the appearance of *Alnus glutinosa* in the fossil record. This is particularly interesting, because at Lochan Doilead *Pinus sylvestris* is only represented for a limited period which post-dates the appearance of *Alnus glutinosa*. The origin of *Pinus sylvestris* pollen in the fossil record from Loch Morar, (whether it relates to local or distant sources) will remain uncertain until future analysis of pollen concentrations is undertaken at this site. Nevertheless, the appearance of this taxon, in the Morar record corresponds broadly with the palaeomagnetic declination feature H (eta), which is dated at *circa* 7400 years BP. A subsequent decrease in *Pinus sylvestris* pollen in the record from Loch Morar corresponds broadly with the palaeomagnetic declination feature E (epsilon), which is dated at 4200 years BP. Bennett (1984) indicates a widespread and severe reduction of this taxon over much of its geographical distribution range within the British Isles by *circa* 4000 years BP.

Significant changes in the vegetation cover and condition of the soils within the catchment area of the Morar Basin during the Holocene Epoch are indicated by the fossil diatom record from Loch Morar. In particular, a relative increase in acidophilous diatom taxa, particularly associated with moorland and *Sphagnum* bog vegetation, is dated at *circa* 7400 years BP. Acidophilous taxa subsequently attain a maximum representation in the fossil record, during the period dated between *circa* 4300 and 2800 years BP. Furthermore, the increase in acidophilous diatom taxa corresponds with a change in the sedimentary succession, indicated by a significant increase in colloidal complexes of Iron (III) Oxide, silicates and humus. These changes are interpreted as representing an expansion of *Sphagnum* bog vegetation and waterlogged soils within the catchment area, during a period when stable isotope variation data indicate particularly wet conditions in Scotland (Bridge *et al.*, 1990). Thus, an increase in the ratio of precipitation to evaporation-transpiration would cause waterlogged or poorly drained ground to become more widespread. Such habitats would favour the development of bog vegetation, particularly on flat and gently sloping sites.

These conditions would be generally unfavourable for the growth and regeneration of Scots pine.

A combination of natural factors, in particular, a relative increase in oceanicity of climate, in conjunction with anthropogenic factors, possibly including localized clearance of woodland, provide the strongest hypothesis to explain the retrogression of the native woodland cover of the Morar Basin during the Holocene Epoch. The broad pattern of events is indicated by changes in the magnetic susceptibility of the sediment succession from Loch Morar and by changing rates of sediment accumulation.

A gradual decline in the magnetic susceptibility of the sedimentary succession from Loch Morar, dating from the beginning of the Holocene Epoch until *circa* 3000 years BP, is accompanied by apparently constant rates of sediment accumulation and suggests a gradual stabilization of the soil cover within the Morar Basin during this period. A gradual increase occurs following a recorded minimum of magnetic susceptibility, dated at *circa* 3,000 years BP, which is accompanied by an increase in the rate of sediment accumulation.

Selective anthropogenic activity, including localized forest clearances as opposed to extensive clearances of tree cover, along with winter grazing by domesticated livestock (dating from perhaps between 4,000 and 3,000 years BP) is suggested as an important factor in the history of the forest eco-system.

Although archaeological evidence of human occupation in this region is sparse, chambered cairns generally dated between 4650 and 3250 years BP and associated with Neolithic-Bronze Age cultures are abundant on the nearby Isle of Skye (Daniell, 1962) and it remains a possibility that people of these cultures may have settled around Loch Morar, although to date there is no evidence of their dwellings or burial sites.

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