ANS.INST. PAT. Ser.Cs. Nat., Punta Arenas (Chile), vol. 19-2, 1989-1990

TIERRA DEL FUEGO AS A TARGET FOR BIOGEOGRAPHICAL RESEARCH IN THE PAST AND PRESENT*

TIERRA DEL FUEGO COMO OBJETO PARA INVESTIGACION BIOGEOGRAFICA EN EL PASADO Y PRESENTE

ABSTRACT

Sakari Tuhkanen[1], Ilpo Kuokka[2], Jaakko Hyvönen[3], Soili Stenroos[3], & Jari Niemelä[4] (1990). Tierra del Fuego as a target for biogeographical research in the past and present. *Ans. Inst. Pat.* Ser. Cs. Nats. 19-2: 5-107 ISSN 0085-1922.

The paper outlines the physical geographical conditions in Tierra del Fuego, the southern extremity of South America in Chile and Argentina, with a series of maps (including some new climatic ones), the composition and affinities of its flora and the principal gradients in the Fuegian vegetacion, examines the history of scientific research of Tierra del Fuego with special reference to phytogeographical research. A Finnish project in biogeographical research of Tierra del Fuego is introduced. An extensive bibliography (about 900 titles) of the geographical, geological and botanical publications dealing with Tierra del Fuego is presented, with special emphasis on contributions by Nordic scientists.

The most decisive physical geographical factor in Tierra del Fuego is the Andean Cordillera system. It brings about abrupt changes of topography and climate in short distances and gives to it a pronounced dualistic character. This is clearly reflected in a sequence of vegetation formations from open moorland and rainforests in the southwest to steppe in the northeast.

Tierra del Fuego, a large archipelago, has been of great interest to various researchers. From the 16th century to our days the character of the exploration has changed into the direction of more scientific inquiry and detailed study. Some of the most important cornerstones in the research have been the first and second Cook circum-navigations (including the biologists Joseph Banks, Daniel Solander, J.R. & J.G.A. Forster), Charles Darwin, Joseph D. Hooker, Per Dusén, Otto Nordenskjöld, Carl Skottsberg, Carl Caldenius, Väiö Auer and his expedtions, Edmundo Pisano and David M. Moore. A series of individual scientists and expeditions have worked in the area and produced a voluminous literature. There are, however, still relatively unknown parts in Tierra del Fuego.

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* Accepted for publication: April 25, 1991.

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The research project of which this paper is the first contribution bears the name "The biogeographical position of Tierra del Fuego in relation to other antiboreal and boreal regions", and an entomological project connected to this is entitled "The occurrence of carabid beetles (Coleoptera; Carabidae) in Tierra del Fuego". Our projects are biogeographically and biologically orientated, when compared to the earlier Finnish expeditions to Tierra del Fuego and southern Patagonia, which were mainly Quaternary geological in character.

The project is connected to the long Nordic research tradition in Tierra del Fuego (cf. the list above). In addition, taxonomic studies of Fuegian cryptogams have been undertaken by Nordic scientists since the last century (E.A. Vainio, William Nylander, Per Dusén, V.F. Brotherus, Veli Räsänen, Rolf Santesson). In zoology there are relatively weak traditions in the research of Tierra del Fuego, espcially as far as terrestrial fauna is concerned, the majority of previous works being more or less inventory in character. In this sense the faunistic-ecological carabid project has a pioneering nature.

Key words: Tierra del Fuego, Chile, Argentina, biogeography, vegetation, history of scientific research, physical geographical background, Southern Hemisphere, expeditions.

RESUMEN

Sakari Tuhkanen, Ilpo Kuokka, Jaakko Hyvönen, Soili Steenroos & Jari Niemelä (1990). Tierra del Fuego como objeto para investigación biogeográfica en el pasado y presente. ***Ans. Inst. Pat.*** **Ser. Cs. Nats. 19-2: 5-107 ISSN 0085-1922.**

Este trabajo esquematiza las condiciones geográficas físicas de Tierra del Fuego, aportando una serie de mapas (entre los que se incluyen algunos climáticos nuevos); analiza la composición y afinidades de la flora y los principales gradientes en la vegetación; examina la historia de la investigación científica, haciendo especial referencia a la fitogeográfica, tanto en ese archipiélago, como en el extremo meridional de Sudamérica en Chile y Argentina. Menciona un nuevo proyecto finlandés en investigación biogeográfica en Tierra del Fuego y presenta una extensa bibliografía (unos 900 títulos) de publicaciones geográficas, botánicas y zoológicas que tratan sobre Tierra del Fuego, dándosele especial énfasis a las contribuciones de los científicos nórdicos.

Considera que el factor físico geográfico más decisivo en el área es el sistema de la Cordillera de los Andes, que produce cambios abruptos en topografía y clima en distancias cortas y le da a Tierra del Fuego un marcado carácter dualista. Ello se refleja claramente en una secuencia de formaciones vegetales que van desde las de tundra rocosa y los bosques pluviales en el sudoeste hasta la estepa en el noreste.

El extenso archipiélago de Tierra del Fuego ha sido de gran interés para numerosos investigadores. Desde el siglo XVI hasta nuestros días el carácter de las investigaciones ha cambiado, desde las primeras exloraciones de carácter naturalista hasta una búsqueda más científica y el desarrollo de estudios más detallados.

Algunas de las bases más importantes para la investigación han sido los trabajos derivados de la primera y segunda circumnavegación de Cook (que incluyeron a los biólogos Joseph Banks, Daniel Solander, J.R. y J.G.A. Forster) y las investigaciones de Charles Darwin, Joseph D. Hooker, Per Dusén, Otto Nordenskhjöld, Carl Skottsberg, Carl Caldenius, Väinö Auer y sus expediciones, Edmundo Pisano y David M. Moore. Una serie de otros científicos individuales y expediciones han trabajado en el área y producido una voluminosa literatura. Sin embargo, quedan todavía en Tierra del Fuego partes relativamente desconocidas.

El proyecto de investigación que se presenta se titula "La posición biogeográfica de Tierra del Fuego en relación con otras regiones antiboreales" y hay en desarrollo otro proyecto entomológico relacionado con él, llamado "Presencia de escarabajos carábidos (Coleoptera, Carabidae) en Tierra del Fuego".

En comparación con las primeras expediciones finlandesas a Tierra del Fuego y Patagonia meridional, que fueron principalmente de carácter geológico del Cuaternario, nuestros trabajos tienen una orientación biogeográfica y biológica.

Este proyecto se conecta con la larga tradición nórdica de investigación en Tierra del Fuego (cf. la lista anterior). En adición, desde el siglo pasado científicos nórdicos han emprendido estudios de criptógamas fueguinas (E.A. Vainio, William Nylander, Per Dusen, V.F. Brotherus, Veli Räsänen, Rold Santesson). Existe, en cambio, una tradición relativamente débil de investigación en la zoología de Tierra del Fuego, especialmente en lo referido a fauna terrestre. La mayoría de los trabajos previos han tenido principalmente el carácter de inventarios. En este sentido, el proyecto faunístico-ecológico sobre carábidos tiene una naturaleza pionera.

Palabras clave: Tierra del Fuego, Chile, Argentina, biogeografía, vegetación, trasfondo geográfico físico, Hemisferio Sur, expediciones.

CONTENTS

PREFACE

The research project, "The biogeographical position of Tierra del Fuego in relation to other antiboreal and boreal regions" presented here, and an entomological project, "The occurrence of carabid beetles (Coleoptera; Carabidae) in Tierra del Fuego" connected with this, have, in a way, a long history behind them.

The first opportunity for the author ST to visit Tierra del Fuego came in connection with another research project, which was realized in Perú in 1984. It so happened that another member in the Peruvian team (IK) was also interested in Tierra del Fuego-in fact, he had earlier prepared a small study on the basis of the material on mires collected by Dr. Heikki Roivainen in Tierra del Fuego in 1928-29. Consequently, after the field work in the Peruvian selva, IK and ST continued to Tierra del Fuego. During a few weeks they collected vascular plants, carried out preliminary field work and made contacts with local research institutions in Ushuaia and Punta Arenas.

The time for the second expedition was to come two years later, during the southern summer 1986-87, this time with the whole present research team, composed of Dr. Jaakko Hyvönen, PhD, Ilpo Kuokka M.Sc., Jari Niemelä, PhD., Sili Stenroos, PhD. and Sakari Tuhkanen PhD. as leader. Our project continues the explorative tradition, so vivid in the Finnish scientific, especially geographic and botanical research in the first half of our century. Our project is biogeographically and biologically orientated when compared to the earlier Finnish expeditions to Tierra del Fuego and southern Patagonia, led by Väinö Auer, which were mainly geological and geomorphological in character, although some botanists also participated.

One of the basic ideas of the Auer expeditions (1928-53) was, however, the same as the incentive for the present project: the idea of comparison of both hemispheres, to compare Tierra del Fuego with ecoclimatically equivalent areas in other parts of the world. In the Southern Hemisphere Tierra del Fuego is almost the only land area, where one can find environmental (and palaeoenvironmental) conditions corresponding to certain parts of Scandinavia.

We hope that our work directly or indirectly can give stimuli to new research, as did Skottsber's and Auer's to us, who some day in the future shall direct their course to this region in order to find answers to new questions or new answers to old questions, although the Fireland they will encounter is no more the Fireland, where Auer with his teams moved and worked, nor is it probably any more the Fireland with which we are so deeply fallen in love. Tierra del Fuego is changing.

The dispositions of this paper and the contents of many parts of it have been discussed by the whole team together. However, ST is primarily responsible for the geological, geomorphological, climatological and pedological parts of the paper, IK for those parts dealing with vascular plants and vegetation, JH for the bryological parts and SS for the lichenological parts. JN's expertise has been utilized in sections dealing with the effects of animals on vegetation.

AKNOWLEDGMENTS

Dreams can turn true. But this dream would never have come true without the support of Prof. Stig Jaatinen and his wife Anita Jaatinen, Prof. Leena Hämet-Ahti and Prof. Teuvo Ahti, who all have stimulated and encouraged us in a magnificent way. Our warmest thanks are due to these persons.

We are indebted to the Museo Territorial of Tierra del Fuego in Ushuaia, to its staff and its Director, Sr. Oscar Pablo Zanola, in particular, for their support and for all the practical arrangements they made for us. Our thanks are also due to Dr. Jorge Rabassa, Director of Centro Austral de Investigaciones Científicas (CADIC), for the facilities his institute offered us and for valuable comments on parts of the manuscript. We also thank Dr. Edmundo Pisano and Dr. Orlando Dollenz, Instituto de la Patagonia, Universidad de Magallanes, Punta Arenas, Chile, for interesting discussions and valuable advice. Sr. Alvaro Sobral gave us good advice and assistance especially in entomological questions.

Sr. Gustavo Giorgis drove us with his minibus on uneven roads and dusty and muddy trails to most difficult places on the main island of Tierra del Fuego.

Ms. Leena Heiskanen, Ms. Iiris Lampila, Ms. Kirsti Lehto, Ms. Pirkko Numminen, Ms. Leena Kriskilä and Mr. Martti Valtonen prepared the figures for publication. Ms. Riitta Kemppainen and Ms. Marjo Kukkola typed a large part of the manuscript. Carol Norris, PhD and Jacqueline Välimäkii, M. Sc., kindly revised the English of the manuscript.

The staff of the Science Library of the University of Helsinki and the staffs of the libraries of the Departments of Geography, Botany and Zoology have kindly assisted us in aquisition of different kind of publications, many of which were very difficult to obtain.

Prof. Teuvo Ahti, Department of Botany, University of Helsinki, read through the manuscript and made valuable comments and suggestions for its improvement.

To all these persons we wish to express our most sincere thanks.

Financial supporta for our project was provided by the Academy of Finland (for the whole team), the Finnish Cultural Fund (IK & ST), the Jenny and Antti Wihuri Fund (IK & ST), the Niilo Helander Foundation (ST), the Oskar Öflund Foundation (JH & SS), the Nordenskjöld Society of Finland (IK & ST) and the Emil Aaltonen Foundation (JH & JN). This financial assistance is gratefully acknowledged.

Helsinki, December 16th, 1990

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Fig. 1. Location of Tierra del Fuego

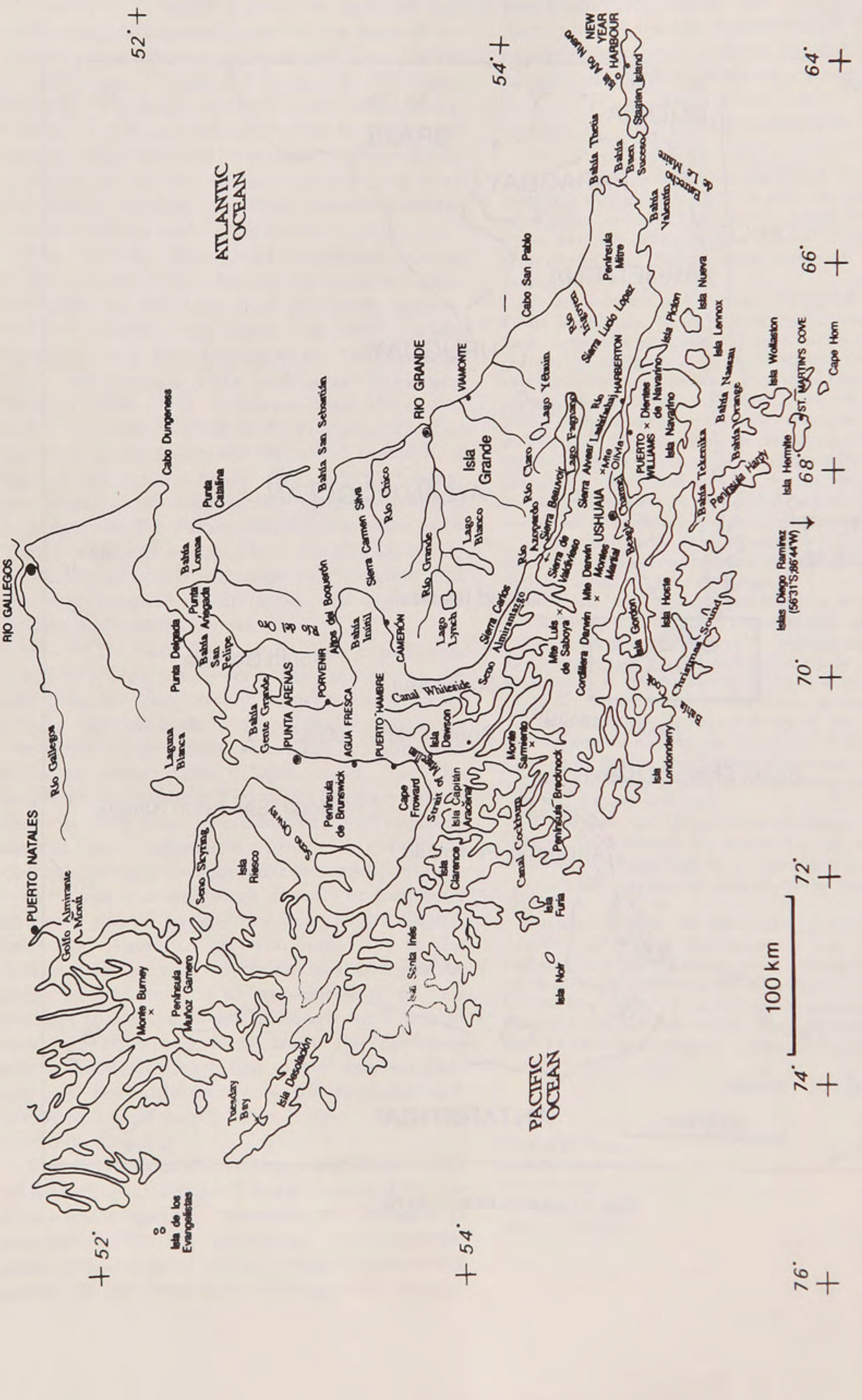

Fig. 2. Fuegian geographic names.

INTRODUCCION

Tierra del Fuego comprises the southernmost part of South America (Fig. 1). It is separated from the South American continent and the South Chilean archipelago by the Strait of Magellan (Estrecho de Magallanes). Tierra del Fuego is a large archipelago, with dimensions of 700 km in the east-west direction and 400 km in the north-south, consisting of Isla Grande (the main island) and a great many smaller islands, among which Isla Desolación, Isla Santa Inés, Isla Clarence, Isla Capitán Aracena, Isla Dawson, Isla Hoste, Isla Navarino and Staaten Island (Isla de los Estados) may be mentioned (Fig. 2). The Beagle Channel separates the main island from Isla Navarino. The well-known group of islands and skeries, Cape Horn archipelago (archipiélago del Cabo Hornos) is located south of Isla Navarino. The Islas Diego Ramírez are an isolated group of small islands about 110 km southwest of Cape Horn (Cabo de Hornos). The total land surface is about 66.000 km^2, 70% of which is taken by the main island.

Administratively, Tierra del Fuego is divided between Chile and Argentina. The border follows the 68°35' W longitude in the north turning then eastwards in the Beagle Channel, so that the small islands of Nueva, Lennox and Picton belong to Chile. The Argentine section forms Territorio Nacional de la Tierra del Fuego while the Chilean section is a part of XII Región (Magallanes y Antártica Chilena), which also comprises western south Patagonia. The population of the Argentina side of Tierra del Fuego is about 60.000 inhabitants, the great majority of them living in the two towns, Río Grande and Ushuaia, the administrative capital of Argentine Tierra del Fuego. Porvenir is the only larger settlement in the Chilean side of Tierra del Fuego with about 5.000 inhabitants. All the outer islands in the west and south are practically uninhabited with the exception of the northern shore of Isla Navarino and, in the Strait of Magellan, the northern part of Isla Dawson.

Originally, Tierra del Fuego was settled by four Indian tribes (Furlong 1917a, Gusinde 1937). The first white colonists came in the 19th century (Canclini 1986). They were missionaries, and after them came gold seekers, other fortune hunters, farmers and tradesmen. Then the annihilation of the indigenous people began. The first sheep farms were established at the end of last century.

The main economic activity in the Fuegian rural landscape is sheep breeding. It is carried out in estancias of even 5.000 hectares or more. There are large areas of southern beech forests in the middle and southern parts of the main island, but commercial forestry is relatively limited, although practised in a very unconcerned way. Oil drilling is carried out in certain places in the northern part of Isla Grande. Nowadays the urban industries in Argentina have surpassed the rural ones in economic significance. Tourism, in particular, has expanded in the 1970's and onwards, and the camping areas are filled with tourists, and big ocean cruisers are often seen in the Ushuaia and Punta Arenas harbours during the summer months.

From the biogeographical point of view Tierra del Fuego is an extremely interesting area. In the Nordic, especially Swedish and Finnish, scientific tradition Tierra del Fuego has played an important role. It is one of the very few land areas in the Southern Hemisphere, where Nordic scientists can encounter environmental conditions comparable with those in certain parts of northen Europe. This is one of the main reasons for the great interest Nordic scientists have shown to this region.

It is not rare that even in global presentations the extratropical portions of the two hemispheres are seen as if they were almost two different worlds. Few efforts are made to demostrate parallelism between the northernmost and southernmost vegetation zones and regions. However vegetation data correlated with climatic indicators can permit to sketch out regions corresponding to Arctic, subarctic, boreal etc. regions in the Southern Hemisphere. Bases for interesting comparisons are then offered by Antarctic, subantarctic and "antiboreal" (term suggested by Koehler 1912, and advocated e.g. by Ekman 1935 and Wace 1965) zone. These zones in both hemispheres can be delimited to be ecoclimaticaly as comparable as possibly, not identical of course, because of the different flora and in part the different physiognomy.

The backbone and the most decisive physical geographical factor in Tierra del Fuego is the Andean Cordillera system which bends eastwards before submerging into the Scotia Sea as the North Scotia Ridge. It brings about abrupt

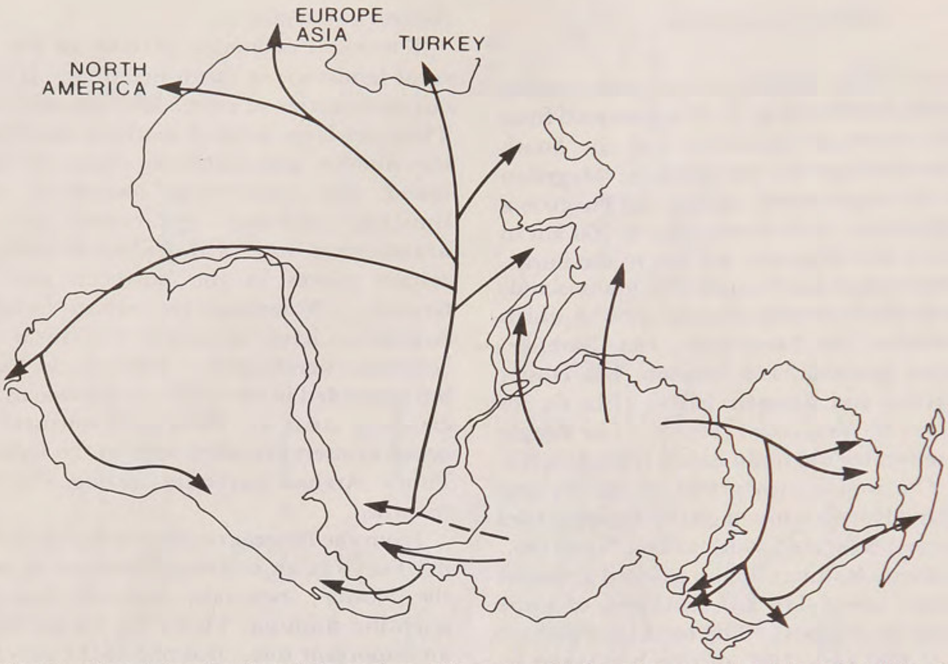

Fig. 3. Gondwana, where Antarctica formed the nucleus. It is presumed to have fragmented and started to drive appart in the Jurasic (about 170 million years ago). The probable migration routes of the heathland flora are shown. Coast lines and continents according to Smith & Hallam (1970), migration routes according to Moore (1970).

changes of topography and climate in short distances and gives a pronounced dualistic character to Tierra del Fuego. Such a steep climatic gradient results in a sequence of vegetation formations from west to east. Bordering the Pacific Ocean there are open moorlands and scrubs. More protected sites in the southwestern inner archipelago are covered by rainy evergreen forests. Towards the northeast these are transformed through mixed forests into deciduous forests. This formation gives way through woodlands to steppes, which prevail in the northeastern part of Isla Grande.

About 150 million years ago the sosuthern supercontinent, Gondwana (Fig. 3), was broken up. The proto-Pacific margin of this continent is thought to have provided ancestors of the austral biota now seen distributed from Tierra del Fuego to Australasia and the circum-antarctic islands.

A relatively undisturbed flora and vegetation (compared to most of near-by Patagonia), great differences in floral origins and physiognomy, as well as the contrasting physical conditions in such a limited area make Tierra del Fuego an optimal place to test and refine phytogeographical theories and hypothesis. One of the special problems is the influence of the extreme oceanity on vegetation, and this fact also makes the comparisons with northern vegetation more complicated. Taken altogeher, Tierra del Fuego is in a sense a phytogeographical laboratory.

The present paper describes the physical geographical features of Tierra del Fuego partly on the basis of all the available literature, partly on our own observations. It sketches the composition and affinities of the Fuegian vascular and criptogamic (excl. fungi other than lichens and algae) flora, and the main gradients in the vegetacion, examines the history of scientific, especially phytogeographical, research in Tierra del Fuego, introduces our research project with field trips in 1986-87. The literature list makes an attempt to be a relatively comprehensive bibliography on the physical geographical and botanical papers published on the Magellanic region.

Because of the ambiguity of several geographical names referring to various regions in southern South America, there is reason to clarify how they are used in the present work:

Fuegia: Tierra del Fuego.

Fuegian archipelago: western and southern islands from Isla Desolación to Cape Horn archipelago including Península Brecknock of Isla Grande.

Fuego-Patagonia: Tierra del Fuego + Patagonia.

Patagonia: southern South America. In Argentina south of Río Colorado (about 40°S), in Chile south of Isla de Chiloé (about 42°S).

Magellanic region: Tierra del Fuego and adjacent regions of Patagonia (south of about 51° S).

As a rule, Spanish geographical names have been used, with the exception of certain well-established English names (Strait of Magellan, Beagle Channel, Staaten Island, Cape Horn, Cape Froward) or names which are almost exclusively known in English because of their historical context (Tuesday Bay, Christmas Sound, New Year Harbour, St. Martin's Cove).

The vascular plant names in the text follow as a rule the nomenclature used by Moore (1983a).

II. TIERRA DEL FUEGO REGIONAL ORIENTATION

1. Location and relief

Tierra del Fuego is located between the latitudes 52° and 56° S, which roughly corresponds to the stretch between Copenhagen and Berlin in Europe. It is the southermost permanently populated area in the world. The northern limits of Tierra del Fuego are 52°42' at Isla Desolación and 52°27' S at Punta Anegada in the east. Between these points the southernmost point of the South American continent, Cape Froward of Patagonia, on Península Brunswick, reaches 53°54' S. The rocky headland Cape Horn, the southernmost tip of Isla Hornos lies at 55°59' S. The longitudinal extremes for the Fuegian archipelago are 74°45' W at Isla Desolación and 63°48' W at Staaten Island. The 1.000 km wide Drake Passage separates Tierra del Fuego from the Antarctic Peninsula. To the east and west vast oceans open.

The Fuegian relief is strongly dualistic. The west, especially that part bordering the Pacific Ocean, is very broken with steep mountains and narrow valleys: an uncounted number of smaller or larger land masses, islands, peninsulas, capes and promontories connected by an innumerable number of waterways, canals, fjords and bays, everything hidden in the persisting mist and rain. This rugged topography has been accentuated by repeated glaciations during the Pleistocene. Not seldom there are glaciers in the mountains, some of which reach down to sealevel. In the northeast the mountainous terrain connects relatively abruptly with the extension of the windy and monotonous Patagonian plain which is dominantly more or less flat lowland, but in minor areas, displays hills and even higher mountains. In the open the plain merges eith descending mountains to form an intermediate region with more gentle and airy features.

Most of the north and east of the main island is undulating lowland under 200 m a.s.l., only parts of the Altos de Boquerón exceeding 500 m (Fig. 4). The area is transsected by the longest rivers of Tierra del Fuego, Río del Oro which runs into Bahía Felipe, and Río Grande which runs into the Atlantic. The main island is dissected by a great depression, occuppied by Seno Almirantazgo (Admiral Channel) and Lago Fagnano. A mountain chain, Sierra Beauvoir and Sierra Carlos, with gently peaks averaging 600-700 m runs along the north side of this depression. The main mass of the Cordilleras lies south of it. The highest parts of Tierra del Fuego are found in Península Brecknock, a derivation of southern Isla Grande to the west: Monte Sarmiento (2.404 m) and in the Cordillera Darwin (Mte Luis de Saboya 2.469 m and Mte. Darwin 2.438 m), the majority of which are covered by a transection glacier. The altitudes gradually diminish eastwards. The highest peaks around Ushuaia reach almost 1.500 m (Mte. Olivia 1.470 m), while Sierra Lucio López at the eastern entrance of the Beagle Channel is under 800 m high. The highest peaks on Staaten Island are about 800 m. The altitudes diminish also southwards (e.g. Dientes de Navarino are 1.195 m). The main part of the Fuegian archipelago lies to the south and west of the highest mountain chain with a belt of maximum elevations about 50-150 km east of the fringe of the western and southwestern archipelago. In the western outer archipelago substantial areas above 500 m occur only on Isla Santa Inés.

This relief zonation has its background in geology, and it is closely related to a parallel climatic, geomorphological, plant-geographical and pedological zonation.

2. Geology

a. Bedrock

The first cscientific observations on the geology of Tierra del Fuego date back to the second half of the 18th century (de Bougainville 1771, 1772, 1783, Cook 1777, see also Beaglehole 1961) and the first half of the 19th century (King 1832, 1839, Darwin 1839, 1842, 1846, 1906, see also Barlow 1934). They included petrological observations and observations on tectonic structure. Many of them were quite meritorious and are still valid. Even then it was suggested that the Andean Cordillera, which disappears into the waters of the Scotia Sea east of Staaten Island, reappears in the Antarctic Peninsula (Barrow 1832). Since those times the structural history and geological formations of the southern part of South American continent has been unravelled by,

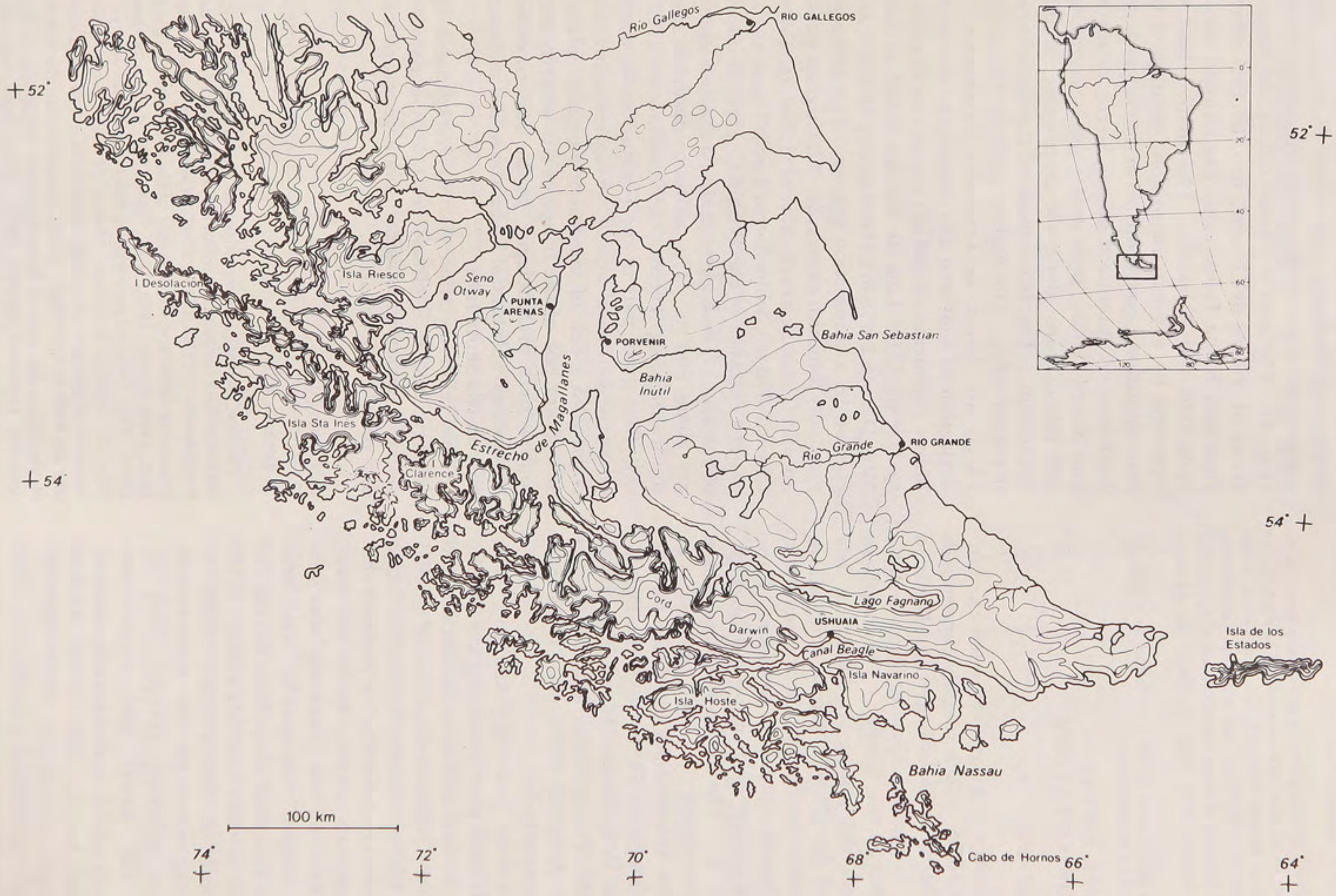

Fig. 4. **Relief of Tierra del Fuego. The contours: at 500 m and thereafter with 500 m interval. Compiled on basis of various** sources, mainly from Butland (1975), Jerez & Arancibia (1972), Goodall (1979 app.) and the available topograhical maps in scales 1:250.000 (Instituto Geográfico Militar de Chile).

for instance, James D. Dana (1854; especially Bahía Nassau), Paul Hyades (1887), Otto Nordenskjöld (1897a, 1898c, d, 1899: geological map on the Magellanic territories, 1907; J.G. Andersson (1907), P. Quensel (1910a, b: coloured map included), G. Bonarelli (1917: geologic map based on a survey of earlier studies; geologic bibliography), E.H. Kranck (1932: coloured geologic map), G.A. Fester (1938a, b, 1939: Fuegian parts of the Central Cordillera) and E. Feruglio (1939: geologic map of southern Patagonia and Tierra del Fuego). A geologic map of the entire South America was published in 1950 by the Geological Society of America (Stose 1950) and in 1964 by UNESCO. A geologic map of Chile in scale 1:1 mill. was published in 1968 by IIG (Instituto de Investigaciones Geológicas, Chile).

The geological teams prospecting for petroleum have elucidated some problems previously unsolved (cf. Thomas 1949). A geologic map in scale 1:500.000 was published in 1978 by ENAP (Empresa Nacional del Petróleo, Chile). Some other geologic maps of Tierra del Fuego and southernmost Patagonia based on ENAP's map or other earlier studies have been published, for instance, by Dalziel & Elliot (1971), Palmer & Dalzier (1973), Winn (1978) and Raedeke (1979). General descriptions of the geology of the whole area are provided by Butland (1957), Russo & Flores (1972) and Borrello (1972), Suárez (1976) discussed the Patagonian Cordillera and Codignotto & Malumian (1981) the pampas area of Isla Grande. The tectonics of the Scotia Arc region, the most obvious link between America and the Antarctic Peninsula (Adie 1963: 458), has been investigated in the Scotia Arc Tectonics Project 1969-1975 (e.g. Dalziel & Elliot 1971, Halpern 1973, Palmer & Dalziel 1973, Dalziel et al. 1974, 1975, Dalziel 1975, De Wit 1977, Dott et al. 1977, 1982, Winn 1978, Winn & Dott 1978).

Southernmost South America consists in general terms of two major geological units: the Andean Cordillera (Cordillera de los Andes), which forms the Pacific and southern side of Tierra del Fuego, and the Magallanes sedimentary basin, or the pampas, the flat and undulating land on the Atlantic side (Figs. 5-6).

The Andean orogenic zone is constituted of the Coastal, Central and Marginal (or Pre-; also called the Sub-Andean belt, Palmer & Dalziel 1973) Cordillera (Nordenskjöld 1898, Kranck 1932, Butland 1957). The Marginal Cordillera belongs to the Magallanes sedimentary basin from a sedimentological point of view, but structurally and tectonically it is a part of the Andean system (Palmer & Dalziel 1973).

The Coastal Cordillera occupies the western and southern flank of Tierra del Fuego from Isla Desolación to Cape Horn and it represents the eroded remnants, the roots, of a volcanic island arc (Dalziel 1975, Dott el al. 1982). It is mainly made up of a great batholit, and is composed principally of acid and semiacid igneous rocks, such as andesites, diorites and granodiorites (so called Andean diorite, a Cretaceous intrusive) and granites (Kranck 1932, Butland 1975, Dalziel 1975).

The Central Cordillera forms the core of the proper Andes representing the preorogenic marginal basin (= back-arc basin). This basin opened in Late Jurassic or Early Cretaceous time and it was infilled bilaterally from the volcanic arc and the South American continent (Winn 1978, Bruhn 1979, Dott et al. 1982; Fig. 7). The Atlantic opened in Early Cretaceous time (Larson & Ladd 1973).

There is evidence to indicate that the volcanic chain, the marginal basin floor and sediment fill, and the rocks on the continental side were tectonically uplifted and penetratively deformed during the Middle Cretaceous about 80 million years ago when the volcanic arc of the Pacific side of the basin moved back toward the South American continent, thus closing the marginal basin in an island arc continent collision (Daziel 1974, 1975, Bruhn 1979, Dott et al. 1982. The deformation and especially elevation of southern Andes are believed to have continued from mid-Cretaceous to mid-Cenozoic time. Through this entire interval, the Magallanes basin subsided rapidly and received water sediments until Miocene time all over but its eastern margin (Springhill Platform; Dott et al. 1982).

The Central Cordillera consists principally of strongly deformed (Palaeozoic to Cretaceous) rocks. Crystalline schists and Palaozoic and Mesozoic sedimentary rocks, which are folded and metamorphosed, cover extensive areas. These schists are penetrated by younger granites or granodiorites in the early Tertiary composing the core parts of the Darwin Cordillera (Kranck 1932: 26, Palmer & Dalziel 1973). Obviously, on the account of its superior resistance to erosion this igneous rock formation constitutes the highest massifs in Tierra del Fuego.

The Pre-(e.g. Bonarelli 1917) or Marginal (e.g. Kranck 1932) or East (Quensel 1910a, b) Cordillera forms a belt of about 50 km in width which emerges along the north side of the Almirantazgo-Fagnano depression. Its rocks are relatively soft and erode more easily, giving the more rounded contours of the mountains. These are formed by Cretaceous sediments-sandstones, clay-slates, marls and especially in the vicinity of the Central Cordillera, conglomerates (Kranck 1932:25)- which underlay the Magellan Tertiary beds (Palmer & Dalziel 1973).

There is a rapid decrease in deformation as

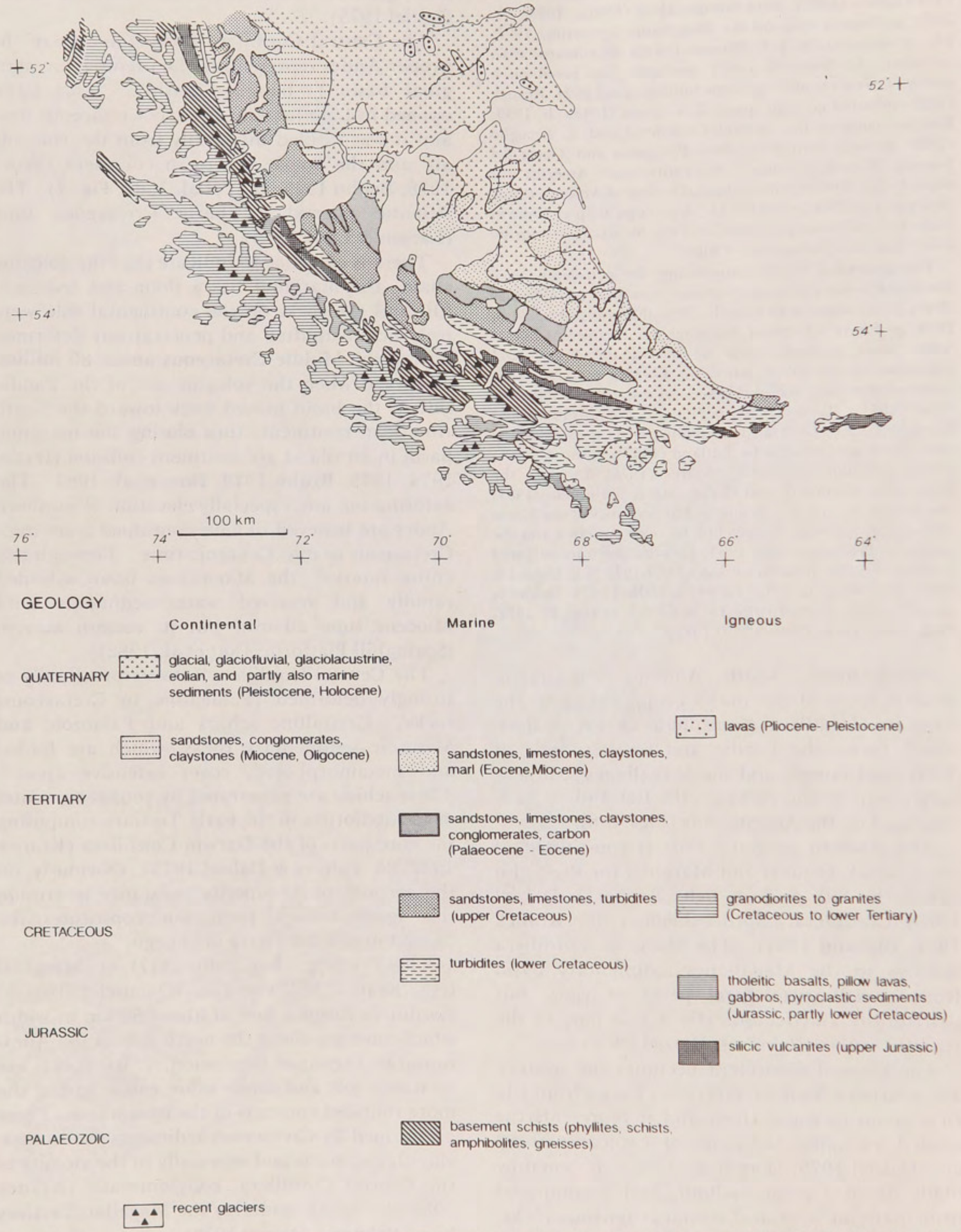

Fig. 5. Geology of Tierra del Fuego. Based mainly on Frederiksen (1988: plate 2) and Palmer & Dalziel (1973: Fig. 2); in the northwest, on Stose (1950), De Witt (1977) and Winn (1978); Staaten Island, according to Dalziel *et al.* (1974).

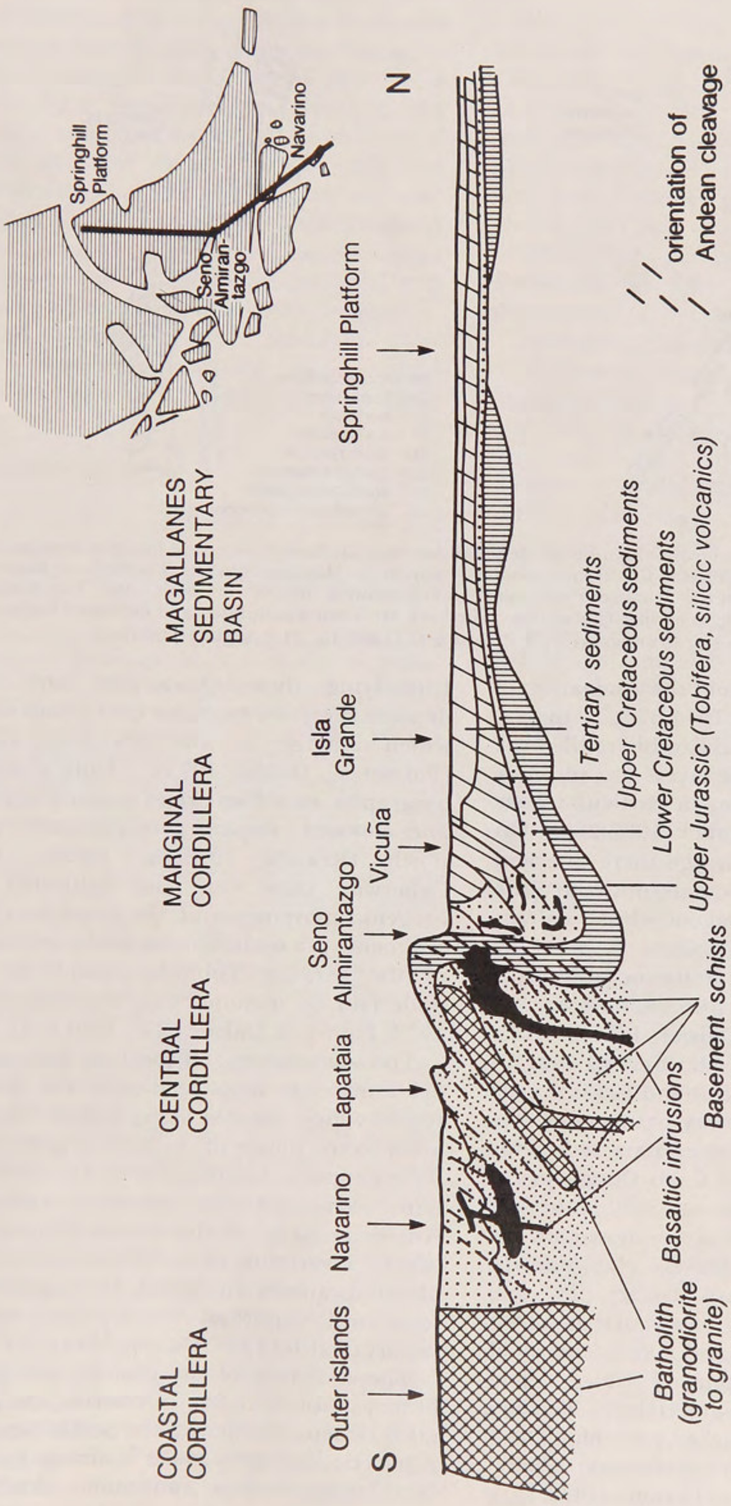

Fig. 6. Schematic north-south cross-section of the Andean Cordillera and the Magallanes basin in Tierra del Fuego. After Palmer & Dalziel (1973, fig. 2), partly modified. Map showing the location of the cross-section in inset.

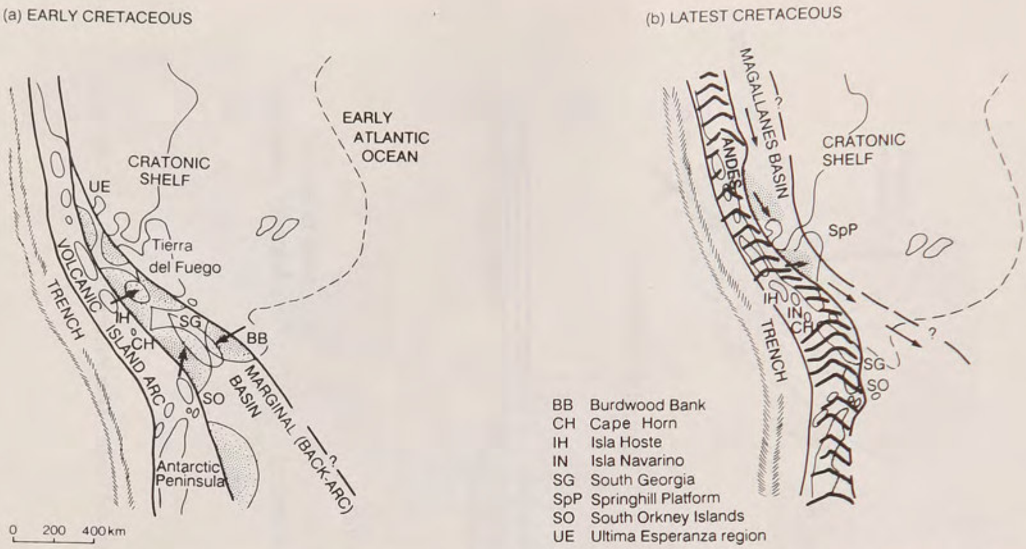

Fig. 7. Palaeogeographic restoration maps of southernmost South America. (a) Early Cretaceous, bilateral deep-sea fans in the back-arc marginal basin, (b) Latest Cretaceous, submarine fans in the Magallanes basin. The back-arc basin opened in Late Jurassic to Early Cretaceous time. It was probably filled by fans growing inward from both sides. The Atlantic Ocean began to form in the latest Jurassic to earliest Cretaceous. The back arc basin was uplifted and deformed beginning in the Middle Cretaceous, and it was closed by 80 million years B.P. Dott & al. (1982, fig. 21,2, slightly modified).

one passes eastward away from the Andean zone (Kranck 1932:25, Dalziel 1974:573). In the western flank of the Marginal Cordillera the beds are strongly folded and the layers are tilted in steep, often vertical positions in particular near the Central Cordillera (Kranck 1932:26). On the western and southern fringe there are acid upper Jurassic volcanic rock outcrops, the Serie Tobifera, overlying the basement schists (Palmer & Dalziel 1973). The Tobifera is probably related to the subduction of the oceanic crust beneath the South American - west Antarctic segment of Gondwana (Dalziel 1975). The sedimentary formations of the eastern margin yield well-preserved fossils (Butland 1957:9).

The Magallanes sedimentary basing proper is covered by Tertiary and Quaternary sediments and in a few places west of Cabo Dungeness in South Patagonia by volcanic material (cones) of Pliocene-Pleistocene age. For the most part the area is overlain by sands, gravels, clays and till deposited by the Quaternary glaciers. In some coastal areas there are also recent marine sands and gravel resulting from the transgressions of the sea during the postglacial time. The Quaternary sediments are underlain by Tertiary sediments in almost undisturbed position. These beds consists of yellowish sandstones, shales, siltstones and conglomerates (Kranck 1932:25).

Underlying these Quaternary and Tertiary deposits there are extensive Cretaceous sediments which emerge at the Marginal Cordillera (Palmer & Dalziel 1973). Only close to the orographic zone they are to some extent lifted up and elevated, sloping gently towards east and north (Kranck 1932:25, Dalziel 1974). Otherwise they were not subjected to the orogenic movements of the Cordillera. These sediments are underlain by acidic volcanic rocks of the Jurassic Tobifera, which in turn is underlain by metamorphic basement (Halpern 1973, Palmer & Dalziel 1973, Dott et al. 1982).

The soutwestern and southern parts of Tierra del Fuego are associated with the Scotia Arc region which, located along a plate boundary, is a key to the puzzle of the former positions of the different parts, i.e. the eastern Antarctic-Australian part and the western African-South American part, of Gondwana relative to each other. The timing of events during the break up of Gondwana in the Scotia Arc region is crucial to several important developments in Earth's history (Dalziel 1975, De Wit 1977).

The similarity of the geology and geological history in southern South America, the continental fragments bordering the Scotia Sea, and the Antarctic Peninsula make it almost certain that there was once a continuous Andean-West

Antarctic Cordillera (Dalziel & Elliot 1971:249, Dalziel 1974:576). The reason for the disruption of the original Cordillera in the Drake Passage is not entirely clear. The predominant factor appears to have been the narrowness of the continental connection between the two parts of Gondwana that are now South America and West Antarctica when the South Atlantic Ocean basin began to open. In all probability the litospheric plate underlying the Pacific Ocean tended to bend and disrupt this continental strip rather than continue to be consumed beneath it. The initial bending of the Cordillera may, therefore, have accompanied rather than postdated the Andean Orogeny (Dalziel & Elliot 1971:250).

b. The Quaternary

Throughout Tierra del Fuego extensive and profound effects, both erosional and depositional features, of the Pleistocene glaciation(s) are seen.

Darwin (1846) was the first to connect certain geomorphologic features with glaciations. Nordenskjöld (1897a, 1898c, d, 1901) made observations on glacial and glacifluvial deposits in Tierra del Fuego. A pioneering and classic study of the terminal moraine systems in Fuego-Patagonia was published by Caldenius (1932 a.b.). The Quaternary history of Tierra del Fuego and southern Patagonia has subsequently been studied by Auer (e.g. 1941, 1946, 1947, 1950, 1956, 1959, 1960, 1965, 1970), Ljungner (1949), Feruglio (1950), Mercer (1965, 1970, 1976, 1982), Raedeke (1978) and Frederiksen (1988). A project entitled "Quaternary of South America and Antarctic Peninsula" integrated with the International Geological Correlation Programme has produced many important contributions on the Quaternary glaciations, the termination of the Pleistocene and the Holocene climatic changes, e.g. Porter et al. (1984), Rabassa et al. (1986, 1990), Heusser & Rabassa (1987), Heusser (1989 a,b, 1990), Clapperton (1990), Rabassa & Clapperton (1990), Clapperton (in press), Porter (in press). Some minor papers dealing with the geomorphology of the northern side of the Strait of Magellan are provided by Marangunic (1974), Uribe (1982) and Prieto (1988 a, b), while Araya-Vergara (1978) dealt with the archipelago of Cape Horn.

Researchers have disagreed about the number of major glaciations during the Pleistocene (cf. Mercer 1965:393-394, Auer 1970: 69-70, Raedeke 1978: 6-7) and about the maximum extension of the Pleistocene ice cover, especially north of Río Gallegos in Argentine Patagonia (Auer 1970: 39). Many apparent misinterpretations have been made.

Caldenius (1932a, b) noted four end moraine belts in Argentine Fuego-Patagonia. By laborious measurements of varve sequences, he correlated the outer three moraine belts with the Daniglacial, Gotiglacial and Finiglacial end moraines of Scandinavia, now known to have been formed between about 20.000 and 9.000 years B.P. His "Finiglacial" moraines in southern South America are those formed during the last major stagnation phase in the retreat of the latest major glaciation. Outside the Daniglacial moraines Caldenius noted other moraines (or an "Initioglacial system") which according to him probably represented older glaciations.

Caldenius, however, underestimated the ages of all these moraines. By means radiometric dating techniques it is now known that the supposed Daniglacial moraines are 177.000 $^{+}$ 57.000 years old, i.e. older than the last major (Würm/Weichsel/Wiscosin) glaciation (Mercer 1982). Caldenius Finiglacial moraines have proved to be slightly older than the European Younger Dryas chron (about 10.000 years B.P) (Mercer 1982).

Frederiksen (1988) correlated the moraine systems in Tierra del Fuego with 5 stages (A...E). Based on Mercer's (1970, 1976) datings, he supposed that the stage E moraines are as old or older than 1-1,2 million years and the stage A moraines slightly older than 12.500 years. Accordingly, the stages B, C and D should be of intermediate age. He postulated that the stage A-C and D moraines belong to the last and second last glaciation, respectively.

There are still many unsolved problems as far as the morainic systems and glacial advances in Fuego-Patagonia are concerned, but it is out of the topic to discuss them in this context. On the basis of the existing literature (Auer 1970, Mercer 1976, 1982, Uusinoka 1987, Clapperton 1990, Rabassa & Clapperton 1990) it can be summarized that during the Pleistocene several glaciations occurred, the most widespread of them prevailing 1,2-1,0 million years ago. During the last glaciation the ice sheet was probably most widespread before 65.000 B.P. And after the interstadial the glaciation peaked during the interval 24.000-18.000 B.P. A rapid recess occurred soon after 14.000 B.P. putting glaciers within their present limits by 11.000 B.P. Mercer (1976) denied the possibility of Late Glacial readvances in the Patagonian glacier about 11.000 B.P., as occurred Scandinavia during the Younger Dryas stade. This was advocated by Hoganson & Ashworth (1981) on the basis of evidence from fossil beetles from Valdivia, but the theory conflicted with Heusser & Streeter's (1980) and Heusser & Rabassa's (1987) data, which suggested that a period of mean annual temperatures as low as during the end of Last Glaciation occurred between 11.300 and 9.400 years B.P. (or between 13.000 and 10.500 years B.P. according to Heusser 1989a, b).

Neoglacial advances have taken place in three episodes, culminating about 4.500 B.P., 2.500 B.P. and during the 17th-19th centuries (Mercer 1976, 1982; Heusser & Streeter 1980). In total, evidence of up to twelve Holocene glacial readvances have been provided (Rabassa 1987).

Consequently, the glaciers receded slightly earlier in Fuego-Patagonia than in Scandinavia. Because of the difference in size of the Scandinavian and Fuego-Patagonian glaciers, the Fuego-Patagonian glaciers have a shorter response time to new climatic conditions than their more extensive Scandinavian counterparts (Mercer 1970, Frederiksen 1988: 21). In any case, it is most probable that the glacial stages during the Pleistocene in Fuego-Patagonia and Fennoscandia correspond to the same climatic events. Even the neoglacial fluctuations have been approximately in line with those in the Northern Hemisphere and New Zealand (Auer 1960, Mercer 1970, 1976, 1982, Grove 1979, cf. also Karlén 1982, Burrows & Gellatly 1982, Rabassa 1987).

The most important accumulation areas of the Pleistocene glaciations were located in the highest mountain massifs of the Central (and Coastal) Cordillera, Cordillera Darwin being primary centre of glacial accumulation in Tierra de Fuego (Raedeke 1978). There was more ice production on the western side than on the eastern side on the Central Cordillera, and so the ice divide was probably displaced west of the topographic divide, i.e. to the Pacific side (Ljungner 1949: 22-23). Secondary ice accumulation centers were located even in the Marginal Cordillera and from these accumulation areas glaciers flowed towards east and south (west) (Fig. 8). Ice descended in broad outlets following pathways such as straits, bays and valleys, especially the Strait Almirantazgo-Lago Fagnano depression, which is clearly reflected in marginal moraine arcs. During the maximum glaciations the ice partly flowed over the passes of the Marginal Cordillera from south and southwest.

During the glaciation periods the temperature was several degrees (even 6-6.5°C) lower than today (Heusser 1989a, b). The were certain fluctuations in the windzones in southern South America (cf. Markgraf 1987b: 156; see also Heusser (1989c), but it is more probable that southern westerlies were dominant in Tierra del Fuego (Ljungner 1949: 23). East of the Andean chain the climate was too dry for accumulation of ice.

During the most extensive Pleistocene glaciation the ice sheet extended to the Atlantic (or, at least, to the present Atlantic coastline) in the area south of Río Gallegos (Nordenskjöld 1898c, Antevs 1929: 693, Caldenius 1932a, b, Groeber 1936, Auer 1958, 1970, Raedeke 1978, Frederiksen 1988), but there is disagreement, if the ice sheet covered the whole of the present Tierra del Fuego. Some very limited areas in the southwestern island groups may have escaped glaciation (Skottsberg 1931) in the same way as it is probable for West Norway (Vogt 1913). North of the Strait of Magellan in western Chile this kind of refugia were obviously more frequent and more extensive. But even in the eastern lowlands and Peninsula Mitre there may have been ice-free areas, as suggested already by Nordenskjöld (1889c: map) and later by Frederiksen (1988). In addition, according to Frederiksen (1988), there were also some ice-free plots in the inner parts of Isla Grande and moreover some nunataks in the Andes. The shelf along the present Fuego-Patagonian coast was in part, at least, ice-free during the "glacio-eustatic" lowering of the sea-level (Auer 1958a: 221, app. I, Auer 1970: 41, van Zinderen Bakker 1970: 34, CLIMAP Project Members 1984).

The development of landforms differend in various parts of Tierra del Fuego due to differences in climate and bedrock topography, and hence in glaciation patterns. In the south and west the glacial relief is mainly of erosional character, on the plains in the northeast is of glacial depositional and glacifluvial depostional and erosional character.

In the west great erosion valleys were carved by Tertiary rivers, the downward cutting power of which was strenghtened by continued uplift (Butland 1957: 17). The glaciation of the region profoundly affected these valleys widenning, deepening and gouging out the network of longitudinal and transverse corridors. Today a bewildering assortment of glacial features can be

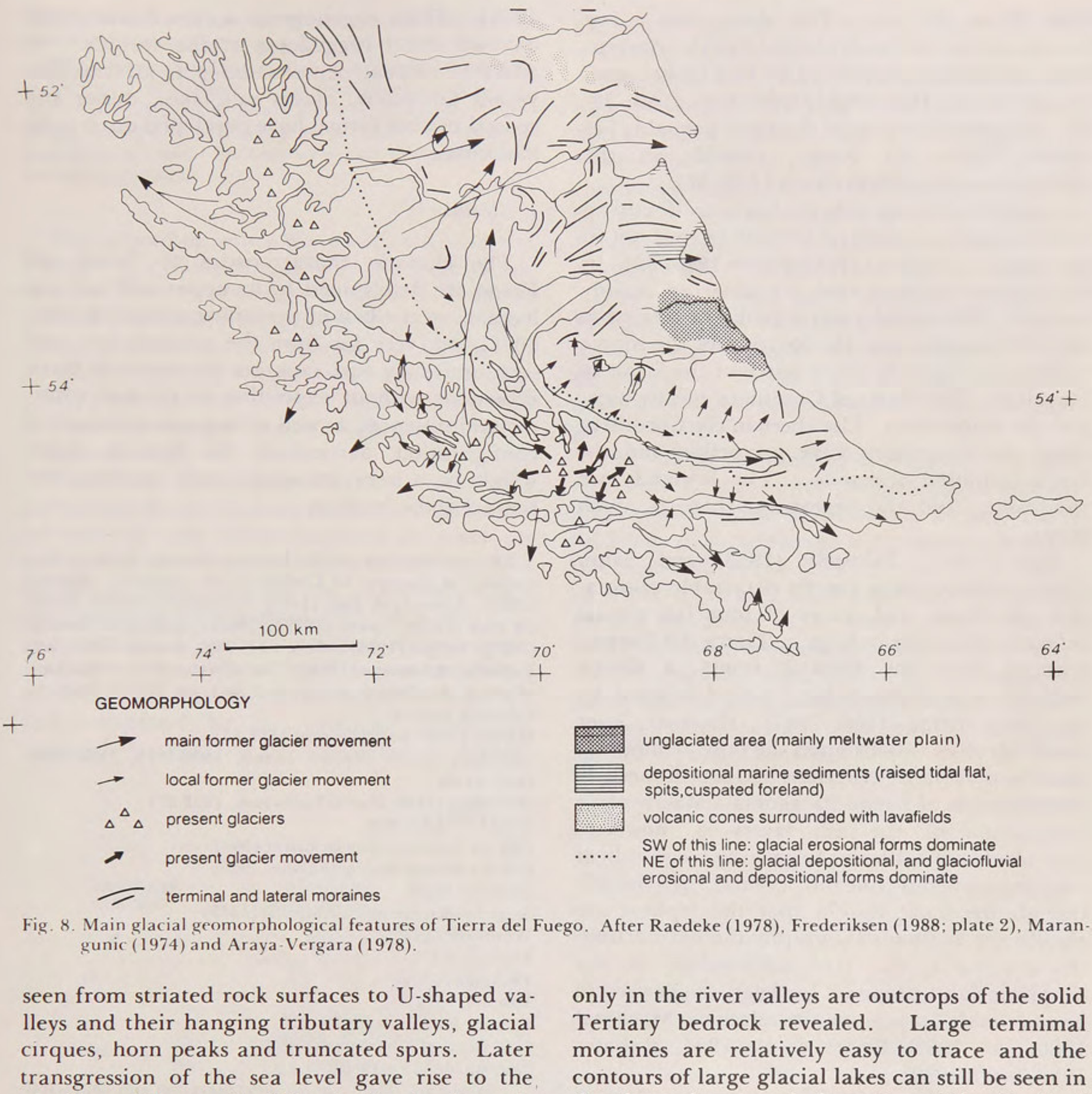

Fig. 8. Main glacial geomorphological features of Tierra del Fuego. After Raedeke (1978), Frederiksen (1988; plate 2), Marangunic (1974) and Araya-Vergara (1978).

seen from striated rock surfaces to U-shaped valleys and their hanging tributary valleys, glacial cirques, horn peaks and truncated spurs. Later transgression of the sea level gave rise to the coastline of thousands of islands, fjords, channels and sounds, resembling the coast of Alaska, Norway and New Zealand.

Today smaller ice-fields following the axis of the Andean mountain zone exist south of the Patagonian ice-field. The largest of these cover an extensive area of the Darwin range, while smaller fields occur on Isla Hoste, Isla Santa Inés and Península Muñoz Gamero.

Towards the east the depositional features of glaciation play a larger role. The broad rounded hills and the undulating lowlands have been covered by a thick cap of glacial debris. Usually only in the river valleys are outcrops of the solid Tertiary bedrock revealed. Large termimal moraines are relatively easy to trace and the contours of large glacial lakes can still be seen in the three-chambered character of the Strait of Magellan between Cabo Dungeness and Isla Dawson (Caldenius 1932a). Lateral moraines in many places reflect glacial pathways. Several terraces indicate stand-still periods in the evolution of glacial lakes while marine terraces indicate that in recent times there has been emergency of this area relative to present sea level.

Norheast of the Marginal Cordillera a silty sheet, probably a loess sheet, is found covering most of the Pleistocene landforms by a continuous blanket, the thickness of which varies from 10 to 125 cm. This sheet with a few exceptions has not been observed in the Andean zone. It has been deposited by late Pleistocene, not during the Holocene (Frederiksen 1988: 30-32). The source region of the sheet probably lies within Tierra del Fuego, possibly in the meltwater valleys (Frederiksen 1988: 32).

Layers of volcanic ash, tephras, are found in the Marginal and Central Cordillera, but not in the Coastal Cordillera (Frederiksen 1988: 32). In the eastern lowlands they are observed mainly in bogs. This distribution is probably related to the windpattern, and the location of the source volcanos in southern Chile north of the Strait of Magellan. The Coastal Cordillera mostly escaped the tephra fans. Elsewhere in the Cordillera zone, the mountains gave protection and the forest inhibited reerosion. The lowlands are windswept, and the vegetation there is much lower.

Auer (1933), Sahlstein (1933) and Salmi (1941) defined three clearly detectable postglacial ash layers and traces of four late-glacial volcanic ash layers in bogs in Tierra del Fuego. Starting from the volcanic layers, a dating method, tephra-chronology, was developed by Auer (e.g. 1933a, 1950, 1947). However, Auer based his observations upon the false assumption that the pyroclastic eruptions had simultaneously covered most of Fuego-Patagonia. Macroscopic comparison of the ash layers is, howerer, apparently not sufficient to permit recognition of contemporaneous volcanic events. All in all, though the basic insight that the tephras are significant as time-stratigraphy marker-horizons remains valid, the tephrachronology in the simplistic form proposed by Auer, has proved to be unreliable for regional correlations (Markgraf 1980a, b. 1983, Porter et al. 1984, Rabassa 1987, Stern 1990).

Acummulation of peat is correlated with rainfall distribution (Auer 1941-, 1963a, Alhonen & Auer 1979), paludification is local and slow in the semiarid steppe area. In the west and southwest most areas are more or less paludified, but the thickest peat deposits are found in the relatively flat and undulating areas near the Marginal Cordillera in the deciduous forest zone, where relief contributes to peat formation and growth of *Sphagnum* is most intense. In these raised bogs, the thickness of the peat layer may be 10 m or more, and it is quite common that the maximum depth bogs is 5 m, at least (cf. Auer 1965). These organogenic accumulations level out the small ruggedness of the terrain. In addition to peat deposits, other landforms like recent alluviums, playas salt lakes, dunes and coastal marine forms, have developed during the Holocene.

3. Climate

The climatic characteristics of Tierra del Fuego are determined by its upper mid latitude location in the belt of prevailing westerlies (40°-60°S), not very far from the Antartic ice, and surrounded by vast expanses of oceans in three directions without exposition to marked continental influences, as well as its geomorphological configuration, particularly the Andean chain, which in a very important way modifies the impact of the location.

This presentation on the Fuegian climate is based on a number of sources: Di Corleto et al. (1946-47), Butland (1957), Almeyda & Sáez (1958), Fuenzalida (1950a, 1967), De Fina (1972), Pisano (1977a, 1983a), Zamora & Santana (1979), Burgos (1985), Weischet (1985), Bondel (1988) and Endlicher & Santana (1988). The climatic data, on the basis of which the climatic maps are drawn, are derived from the following sources:
Martial (1888: Bahía Orange 1882-83)
Skottsberg (1909: Staaten Island, 1886-1893, 1886-1893, 1895, 1896).
Skottsberg (1916: Puerto Harberton, 1903-07)
WMO/OMN (1962)
Oficina Meteorológica de Chile (1964)
Oficina Meteorológica de Chile (1966)
De Fina (1972)
Servicio Meteorológico Nacional (1972)
Wernstedt (1972)
Miller (1976)
Prohaska (1976)
Pisano (1977a)
Zamora & Santana (1979)
U.S. Dept. of Commerce (1982)
Instituto de la Patagonia (s.a.)

The main difficulty in the interpretation and characterization of the climatic features in Tierra del Fuego is the lack of a sufficient network of meteorological stations with reliable records functioning over a long time. The most reliable data from the Magellanic region exist for Punta Arenas (from 1888), Río Grande, Ushuaia and islotes Evangelistas. They are, however, all located near the coast so that they do not represent well contidions in the interior parts of Isla Grande or in the mountains. There are no records for any considerable period from these areas. For this study records from a total of 30 observation points were used, and the maps were drawn from unreduced values, so that they represent the actual conditions prevailing at the altitudes of the stations themselves. In most cases stations are situated near to sea level. An attempt was made when drawing the isopleths to take into account the topographical configurations (although this was not possible to any considerable degree in the west and south), and the direction of channels.

Only a few stations have an observation period of as much as 30 years. Accordingly, it has been necessary to rely on shorter periods when these are ten years or longer. Points whose observations were based on periods of less than ten years have been used. But these were taken into account only as rough guidelines.

The prevailing winds are associated with the passage of cyclons throughout the year in an east-southeast direction across the southernmost part of the continent (Arnett 1958; Fig. 9). These depressions are formed on the South Pacific Polar front, which develops in the region about longitude 110° to 120°, between two cells of South Pacific sub-tropical high pressure belts (Taljaard 1972).

Tierra del Fuego and southern Patagonia, particulary in winter, sometimes come under the influence of cold stable Antarctic air when an anticyclone or a ridge of high pressure develops behind a series of depressions. This results in a cold southerly air stream of Antarctic origin causing brief sunny, but dry, cold, usually windy periods of weather. More often, however, on passing northward, this Antarctic air is rapidly warmed and moistened by the relatively warm sea surface. It thus reaches the region as a cool, moist and unstable current entering into the westerly cyclonic circulation.

The West Wind drift, which encounters the region from the northwest, exerts a pronounced oceanic mildering tendency in winter along the whole Pacific seaboard. Ice cover in the channels is unknown. The northward Falkland current of cold water from the south along the Atlantic coast has a cooling influence and contributes to the cooler conditions in estern Tierra del Fuego and southern Argentine Patagonia. The direct oceanic influence penetrates strongly along the Strait of Magellan, thus separating two "cloud nuclei"; in southern Patagonia and on the main island of Tierra del Fuego.

The direct influence of oceanity is seen especially in the winter temperatures (Figs. 10 and 11) with almost all the coastal areas of Tierra del Fuego showing average temperatures above the freezing point in the coldest months. However, only the high mountain areas are exposed to freezing conditions; in the inner parts of the main island the mean temperature in midwinter is below freezing even in the lowlands. The temperature gradients around the cold cores are relatively steep, wehereas there is no evident gradient in the north-south direction.

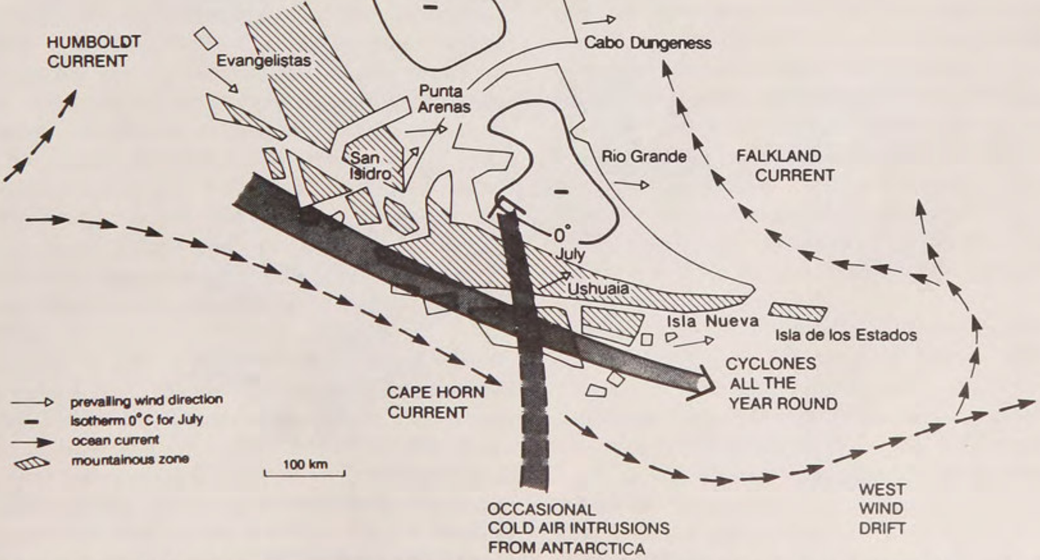

Fig. 9. Prevailing winds and ocean currents in Tierra del Fuego and adjacent regions. Wind directions after Zamora & Santana (1979), ocean currents after Knox (1960), temperature data from the sources mentioned in the text.

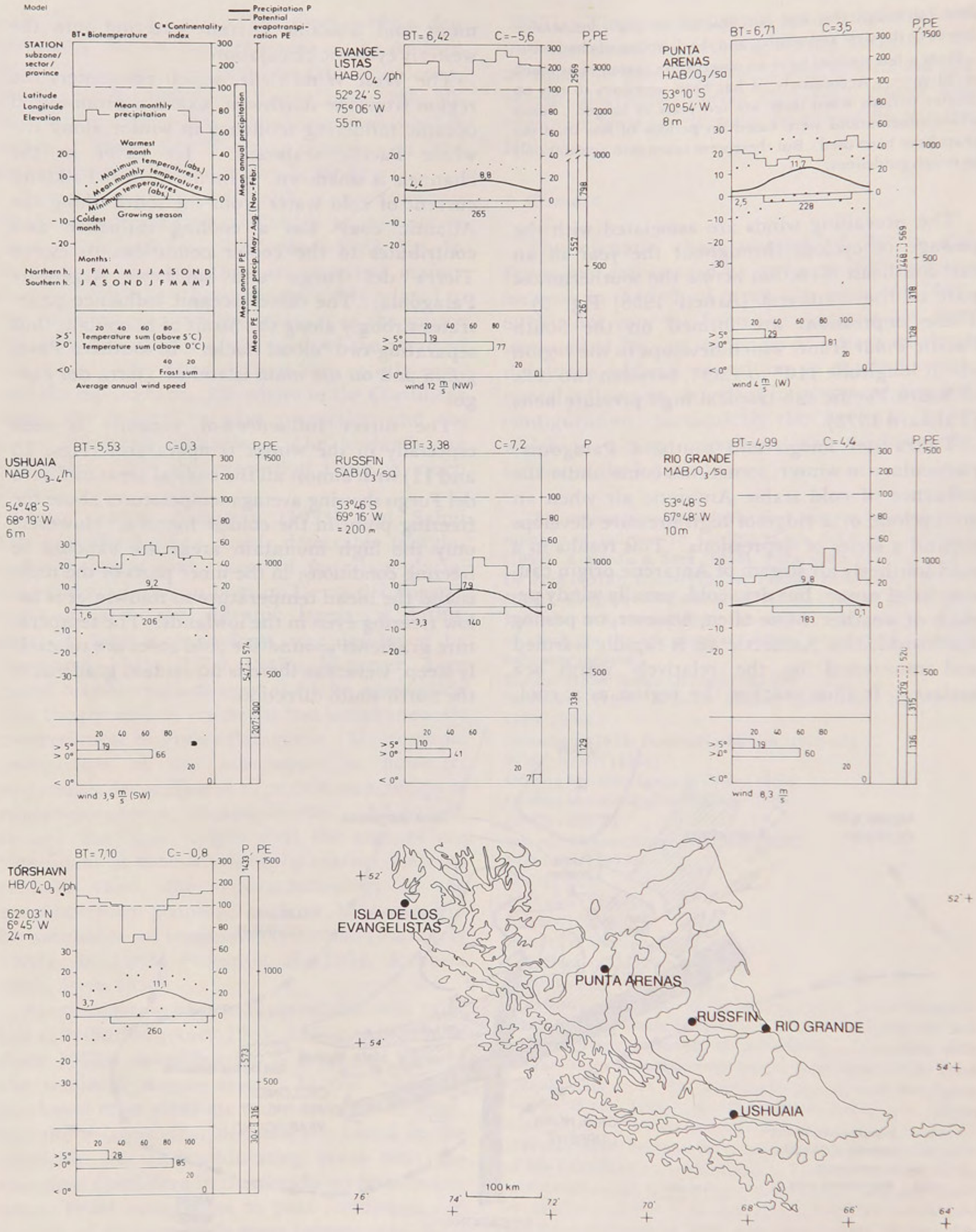

Fig. 10. Climatic diagrams from Punta Arenas (Miller, 1976), Río Grande (Wernstedt, 1972), Ushuaia (Prohaska, 1976), Islotes Evangelistas (Miller, 1876) and Rusffin (Instituto de la Patagonia, s.a.). The diagram for Torshavn, Faeroe Islands, (Lysgaard, 1979), is shown for comparison. Keys are given at the upper left corner.

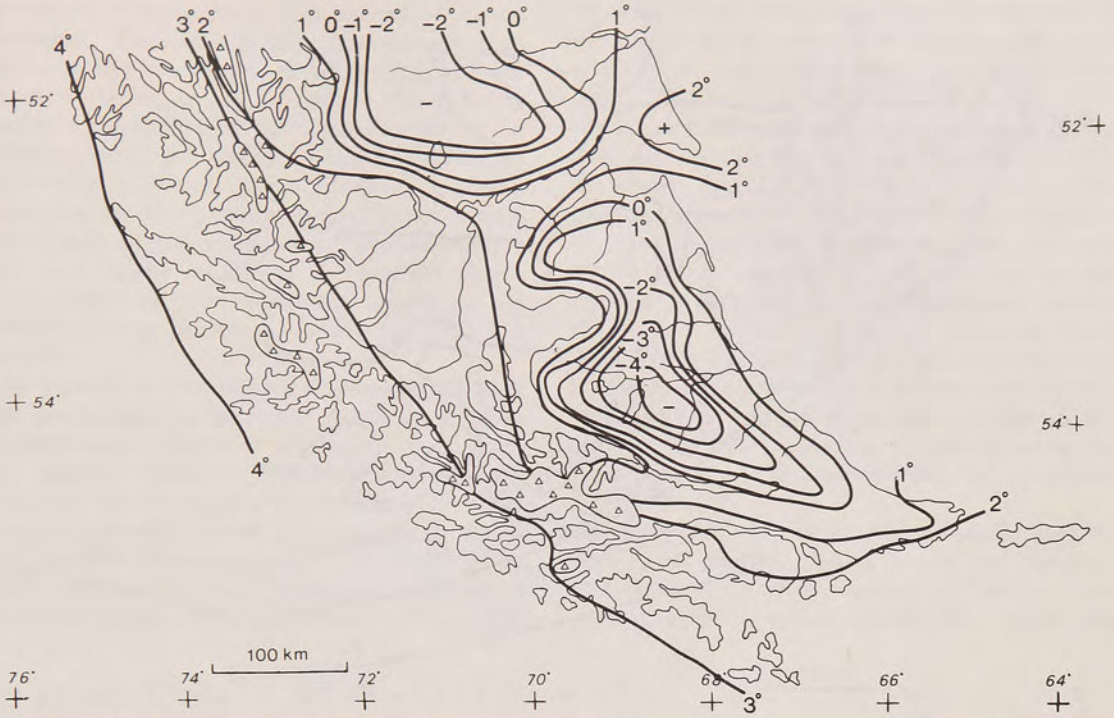

Fig. 11. Mean temperature (in °C) for the coldest month (as a rule, July, but August in the most oceanic stations of the extreme south-west). The temperature gradients around the cold cores (cf. Fig. 9) are relatively steep, whereas there is no evident gradient from north to south. Map based on the sources mentioned in the text.

Summer conditions (Fig 12) show the slight continental influence of Argentine pampa of the northeast. The south-west fringe of the Fuegian archipelago experiences the coolest summers. There is an evident gradient in the mean temperatures for the warmest month of the year from west to east along the oceanity gradient (Evangelistas 8,8°C, Punta Arenas 11,7°C, Río Gallegos 12,4°C) and also from north to south (Puerto Natales 11,4°C, Ushuaia 9,2°C), which gradients partly join the oceanity gradient. All in all, this deficiency of summer heat, or lack of really warm summers, is one of the most noticeable features of temperature conditions in the region.

As far as the vertical temperature gradients are concerned, there are few records available from Tierra del Fuego or southern Patagonia. But according to Laaksonen (1976) the mean vertical temperature gradient in Fennoscandia is 0,53°C/100 m, which agrees well with the results obtained in many other studies. On the basis of their study in Jujuy and Salta provinces in Argentina, De Fina & Sabella (1960) decided on a value of 0,50°C/100 m. Of course, there is so much climatic veriety in Tierra del Fuego that a single value for vertical temperature gradient fails to provide a very correct indication of conditions in different parts of the region at different seasons and the differences for mountain massifs exposed directly to the western oceanic influence versus the more protected ones. in any case, the value of 0,5-0,6°C/100 m is a good guideline. This means, for example, that the mean temperature would be about 6°C in the vicinity of Ushuaia at the altitude of 600 m (corresponding to the timber line) in January and about -1,5°C in July.

The impact of relatively higher degree of continentality in the form of higher summer temperatures is not experienced in the interior of the main island. The inner parts of the main island are climatically the most unfavourable, both in winter and summer. The atmospheric instability stemming from strong winds renders this kind of compensation impossible (Bondel 1988). Data on temperature conditions in the inner parts of the main island north of the

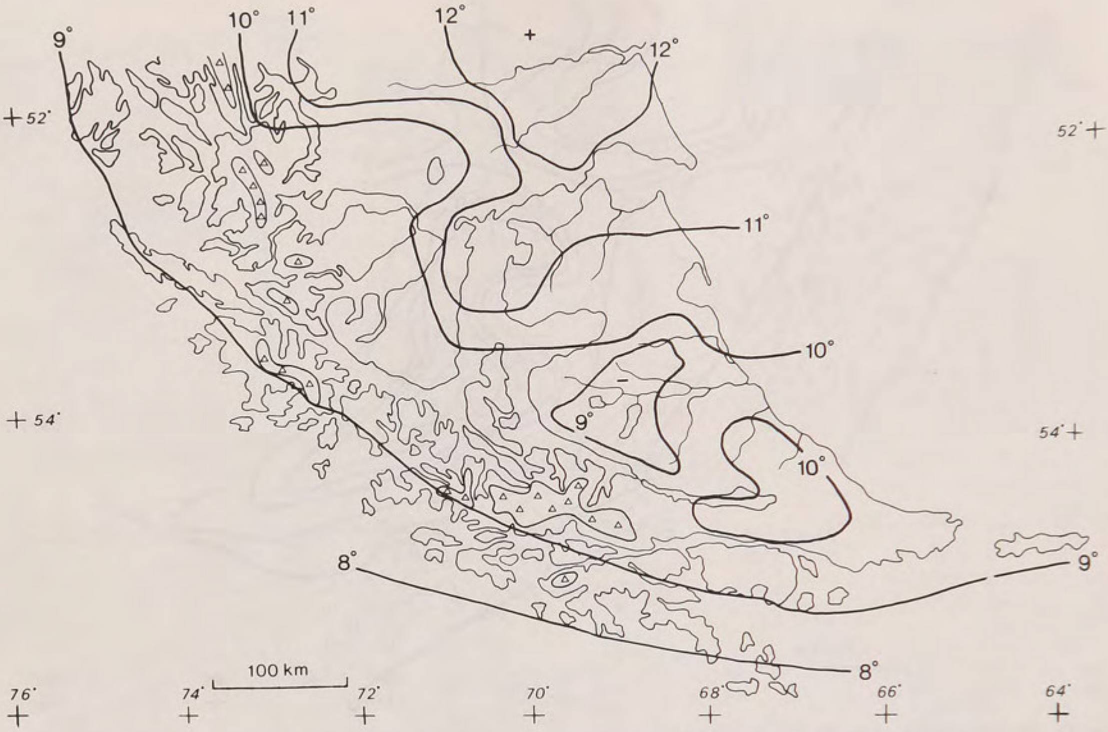

Fig. 12. Mean temperature (°C) for the warmer month (as a rule January, but perhaps February in the south-west and west). No steep gradient occurs. Map based on the sources mentioned in the text.

Almirantazgo-Fagnano depression are nevertheless unrealiable and perhaps do not represent well conditions especially in the forested area. Vegetation characteristics suggest that the temperature conditions might not be so unfavourable as depicted by the climatic maps. The foehn effect on temperature conditions seems to be neglible, probably because most of the Fuegian Central Cordillera and especially the Marginal Cordillera are too low (Eriksen 1979).

Obviously, with such seasonal conditions no great ranges of temperature occur. The difference between the mean temperature of the warmest and coldest month of the year reflects degree of oceanity. In the west the difference may be only 4-5°C, in Ushuaia it is 7,6°C and in Río Grande 9,7°C. The biggest difference is found in the inner parts of the main island, where it may reach 13°C.

The temperature conditions in the region rarely are extreme. The absolute maxima and minima temperatures in °C are as follows: Islotes Evangelistas max. +18,8°, min. -7,2° (period 1914-70), Punta Arenas max. +29,0°, min. 9,3° (period 1930-85), Ushuaia max. +29,0°, min. -19,6° (period 1914-60). The average daily ranges of temperature are also small: Islotes Evangelistas 3,5° in July (i.e. mean daily minima above zero) and 4,6° in January (i.e. mean daily maxima a little higher than 11°), Punta Arenas 4,6 in June (i.e. mean daily minima about zero or slightly below) and 8,3° in January-February (i.e. mean daily maxima 14-15°). On an average, the lowest temperatures recorded annually are about -3 to -2 on Islotes Evangelistas, -5 to -6 in Punta Arenas and -7 to -9° in Ushuaia. The highest temperatures in summer are about 16°, 23° and 24°, respectively.

On account of the relatively even temperature regime, the thermal growing season (daily mean temperatures +5°C or above) is quite long, although cool, especially in the west and along the coast of the Strait of Magellan and the Beagle Channel (Fig. 13). In the west the daily maximum temperatures often exceed 5°C even in winter. The unfavourable temperature conditions in the inner parts of the main island are clearly reflected in the length of the growing season: while the length may be 8 months on the western islands, it is only 5 months in the central parts of Isla Grande north of Sierra Carlos. Frosts during the growing season occur in the inner parts of the main island probably every year even in the middle of the summer (Serra 1970), while on the coasts the length of the screen-frost-free season is usually at least 2-3 months.

As a result of the relative positons of the high and low pressure areas in the South Pacific and South Atlantic, the dominant winds come from the western sector. At most stations, the northwest or west are recorded as the most frequent wind directions. Cold southerly winds are sometimes experienced, particularly in winter, because of the northward movement of polar air masses. The prevalence of the strong westerly winds in combination with chilliness is undounbtedly the most unpleasant feature in the climate of Tierra del Fuego, and at the same time an importan plant-ecological factor. The winds are more persistent and stronger in spring and summer (September to January) and less so in winter, but the difference is small. The frequency and strength of the winds in summer explains to a high degree the cool summer conditions in the region. Particularly in the mountainous channels local influences modify the general wind direction. A turbulent local wind which blows down into the channels from the islands and mainland, is known as williwaw. It occurs especially in spring and summer. It is of short duration, and these squalls of hurricane violence are often accompanied by torrential downpours.

In the west the mean annual wind speed is 12m/s, no month is below 9 m/s and maxima exceed 30 m/s every month. Due to the sheltering effect, mean annual wind speeds are

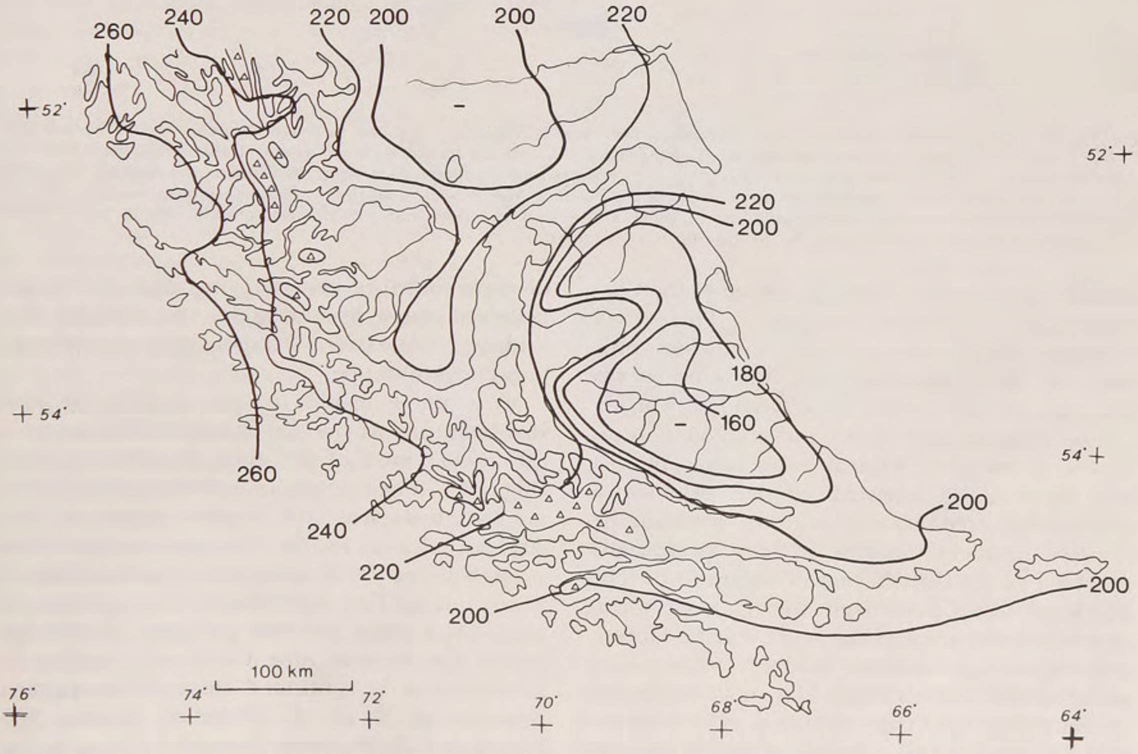

Fig. 13. Thermal growing season (delimitated on the basis of dayly means over 5°C). In the west and along the Strait of Magellan and the Beagle Channel, even if cool, it lasts up to 8 months; in interior localities it lasts 5-6 months, and might be warmer than in the west. Calculated on the basis of monthly mean temperatures (sources given in the text), which might cause an error up to 10 days. Daily mean temperatures were not available.

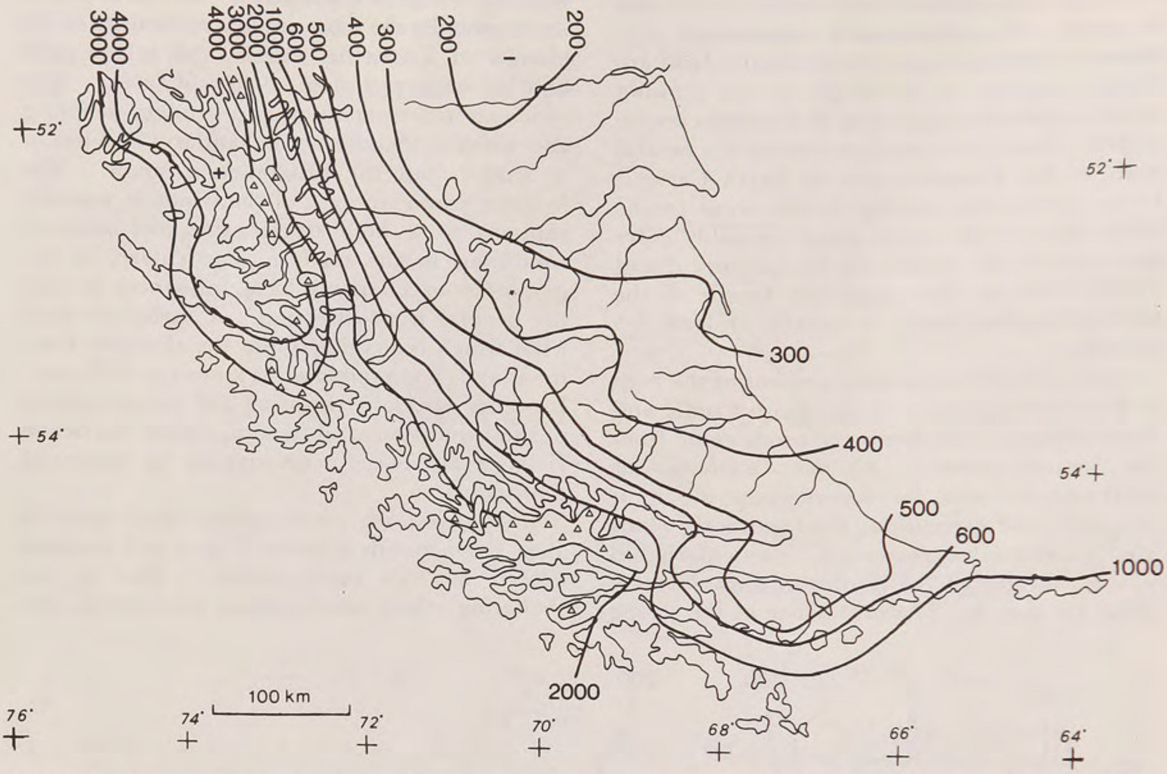

Fig. 14. Annual precipitation in mm. There is a pronounced west-east gradient as shown by the intervals between isohyets 0-500 mm and 1.000-4.000 mm respectively. The highest ammounts are recorded on the western flanks of the main chain of the Central Cordillera. There are several cartographic interpretations of precipitation from the Chilean and Argentinean sides of Tierra del Fuego, but the isohyets do no coincide at the border. Map based on all the available precipitation data (sources mentioned in the text), taking into consideration the prevailing wind directions and probable topographic effects, and to some extent, the evident information given by the distribution of vegetation.

about 4 m/s in some places in the lee of the Cordillera (e.g. in Punta Arenas). This effect decreases with distance from the orographic zone: on the Patagonian coast line wind speeds reach an average of 8 m/s (Río Grande 8,3 m/s).

The pressure and wind conditions in association with the great Andean orographic, mainly N-S or NW-SE oriented barrier produce a contrasting precipitation pattern, a dramatic rainfall gradient, which is very profoundly reflected in the distribution of vegetation. The dominant winds come from the relatively warm and temperate areas of the South Pacific Ocean, carrying a high moisture content. When they arrive at the western coast, this moisture begins to condensate and is precipitated as rain on the lowland areas of the archipelago and as snow on the mountains. The outer islands do not receive such a heavy precipitation as the inner parts because of their lower relief. After precipitation of their moisture content, the winds follow an eastward course becoming dry and inducing the aridity of the eastern Patagonian and northeastern Fuegian steppe.

It is not possible to give a detailed and realibale map of the distribution of the precipitation, but most of the main features are clear (Fig. 14). The highest amounts of precipitation are reached near the highest peaks of the Andean chain; in the Patagonian ice fields probably even 7.000 mm or more (Schwerdtfeger 1956) but in Tierra del Fuego the maxima are probably 4.000-5.000 mm per year. In the lee of the Cordilleran zone the steady decline in precipitation is continued towards the eastern mounth of Strait of Magellan (below 300 mm/year). In southern Tierra del Fuego, in the eastern part of the main island and on Staaten Island, the few records that exist are very unreliable and based on short observation periods. It is not impossible that the precipitation in the eastern tip of the main island is considerably higher than depicted on the map. In southern Tierra del Fuego it is evidently less than on the western islands, mainly because the mountain ranges are not aligned transversely to the prevailing wind.

As regards to the seasonal distribution of the precipitation there is no dry season in Tierra del Fuego or southern Patagonia. Rainfall is received at all seasons, the maximum occurring usually in the autumm, minimum in the spring. The seasonal differences are naturally of greater significance in the rain shadow area (e.g. Río Grande 21 mm in August, 52 mm in March) than in the rainy zone (e.g. Evangelistas 276 mm in March and 170 mm in November).

The distribution of the amount of precipitation is correlated with the number of rainy days. Not only is the western archipelagic zone one of very high rainfall, but of persistent cloudy rainy weather, rain occurring on at least three days of four. At the western entrance of the Strait of Magellan, at Islotes Evangelistas, there is no month with an average of more than five days without rain and the mean cloudiness is 85-90% at all seasons. The rainfall in this zone falls largely in the form of a driving, dizzly, fine rain, lasting for hours, often for days, or even weeks, although downpours of heavy rain are also quite common. The frequency of rainy days decreases to one of four or five in the driest areas, and mean cloudiness decreases to about 65%.

Snow does not normally remain long on the ground near the sea level, particularly in the coastal areas. However, in the mountain zone, and in the inner parts of the main island, there is permanent snow cover of longer duration. On the other hand, practically everywhere in Tierra del Fuego, at aleast once every ten years, a day of snow fall may be expected in the middle of summer (Weischet 1985). The period during which smaller lakes and ponds are ice-covered may last months in the inner parts of the main island. It is not unusual that the whole surface of Laguna Escondida (a few kms south of Lago Fagnano, about 200 m.a.s.l.), for instance, freezes (Bondel 1988).

On average, days with snow fall are only 10 per year in Río Grande in the northeastern coast, because of the small amount of precipitation especially in winter. In Ushuaia the number is 50 and at Evangelistas 20. The central part of the main island is largely snow-covered from May to September (Bondel 1988). In the coastal areas there is probably no permanent frost in the ground and it is never deep. Skottsberg (1909:8), for instance, noted that there was no frost in the ground in the beginning of October just after the disappearance of snow cover. The permanent snow line in the mountains is at about 700-1.000 m.a.s.l., although the local variations are great. At several places in the west glaciers stream down to the sea.

Climate and plants. Taken altogether, certain requirements are made upon the ecological amplitude of plants on account of the specific climatic conditions in order to thrive in different parts of Tierra del Fuego. Plants should be able to utilize the long, cool growing season (which in the westernmost archipelago lasts all year round, in practice), i.e. they should be able to go through their whole life cycle under cool conditions. They should be able at most sites to cope with the almost constant and often strong wind. There is a very pronounced difference between sheltered and exposed sites.

In the west and south-west and in other parts of Tierra del Fuego exposed to direct oceanic influence the plants need not be equipped to withstand intense cold or long periods of subzero temperatures or deep frost in the ground. Very high maximum temperatures (above 25°C) are not experienced in the west and southwest, and in areas where they occur they are of relatively short duration and occur seldom. In most parts of Tierra del Fuego plants need not to be adapted to intense drought, but in the northwest, taking the desiccation effects of strong winds into consideration, xerophytic adaptations are necessary. In the same area winter conditions with normally only a thin snow cover constitute a critical factor for many plants.

Ecoclimatic counterparts. The combination of differente climatic elements is so specific in Tierra del Fuego that other parts of the world have only very limited areas with more or less equivalent climatic conditions, i.e. ecoclimatic counterparts or "homoclimates" (Tuhkanen 1990; Fig. 15). It is of course very decisive for the determination of equivalent climates how narrowly they are defined. In the following the basis is the climatic-phytogeographical regional system, in which the principal climatic gradients (amount of warmth, oceanity/continentality,

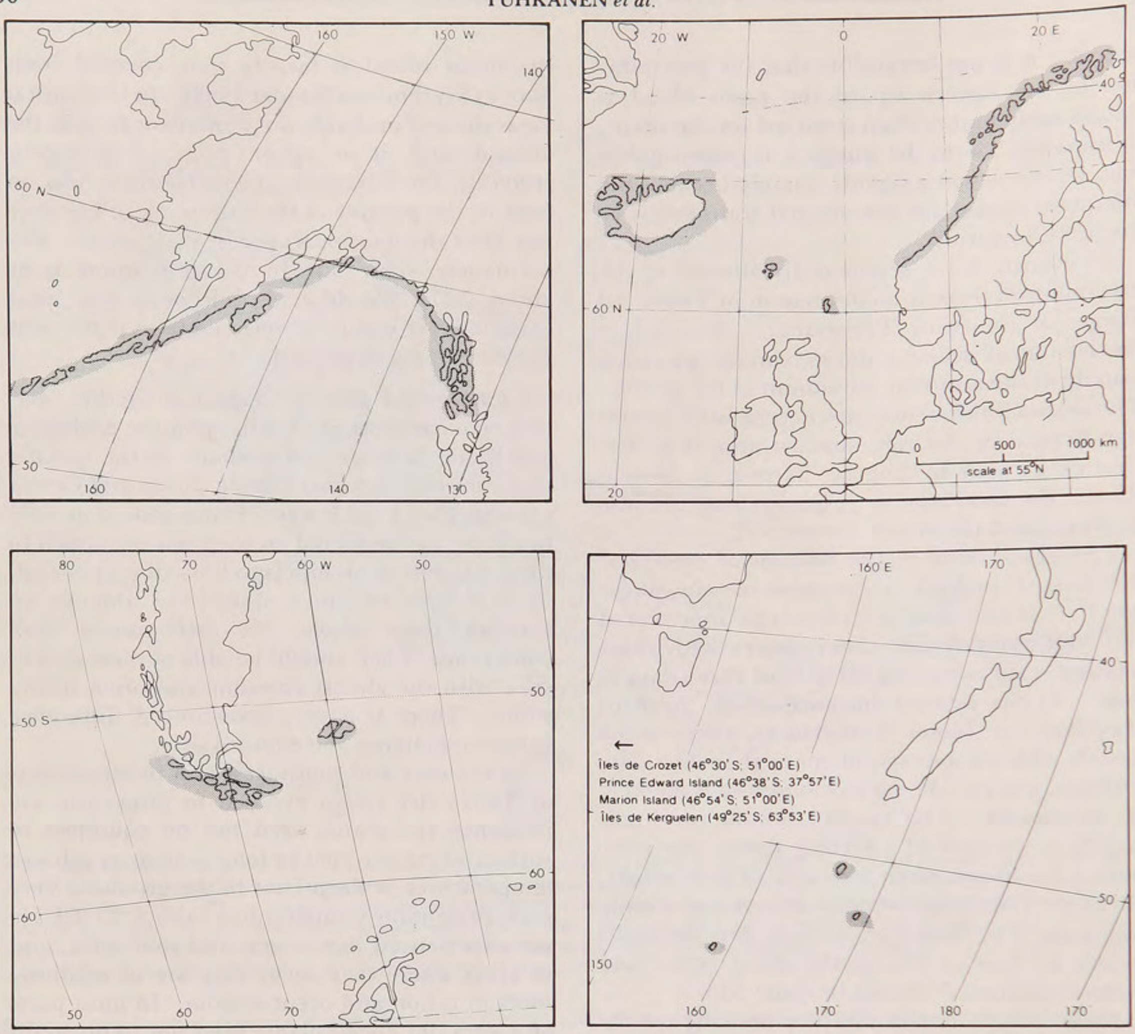

Fig. 15. Ecoclimatic counterparts of Tierra del Fuego. Location of areas of comparable climates (mountain climates largely ommited), contructed on basis of three principal climatic gradients: amount of warmth, oceanity/continentality and humidity/aridity. There are no counterparts elsewhere for the semiarid parts of Tierra del Fuego (Tuhkanen, 1990).

aridity/humidity) are used and quantified by means of certain climatic parameters and indices (cf. Thkanen 1984, 1986, 1987, 1989, 1990a). Without describing the system in more detail in this context, it can be stated that the requirement for the degree of climatic similarity is relatively high.

In the Southern Hemisphere the Auckland and Campbell Islands south of New Zealand and certain other southern island between the latitudes 40° S and 60° S constitute ecoclimatic counterparts in relation to the western Fuegian climates as represented by Islotes Evangelistas. They are all extrememly oceanic, very humid and windy places.

In the Northern Hemisphere there is a narrow coastal strip in the Alaska Panhandle and on the southern coast of Alaska, very humid and very oceanic, although not so oceanic as those parts of Tierra del Fuego where the amount of precipitation is as high as there. Winters in Alaska are colder than in the Pacific archipelago of Tierra del Fuego.

In Europe the closest counterparts are found on the western coast of Norway. Summers are, however, warmer than in Tierra del Fuego, because of the continental effect of the Scandinavian land mass. Tórshavn on the Faeroe Islands and Punta Arenas show very similar thermic conditions, but as regards humidity contidions, Punta Arenas is much drier. The same is true in comparison between Reykjavík on Iceland and Río Grande. But very probably parts of the south Icelandic coast and the southern and eastern coast of Península Mitre and perhaps Staaten Island correspond closely to each other. All these European counterparts are located at considerably higher latitudes than is Tierra del Fuego.

The eastern coasts of North Asia and North

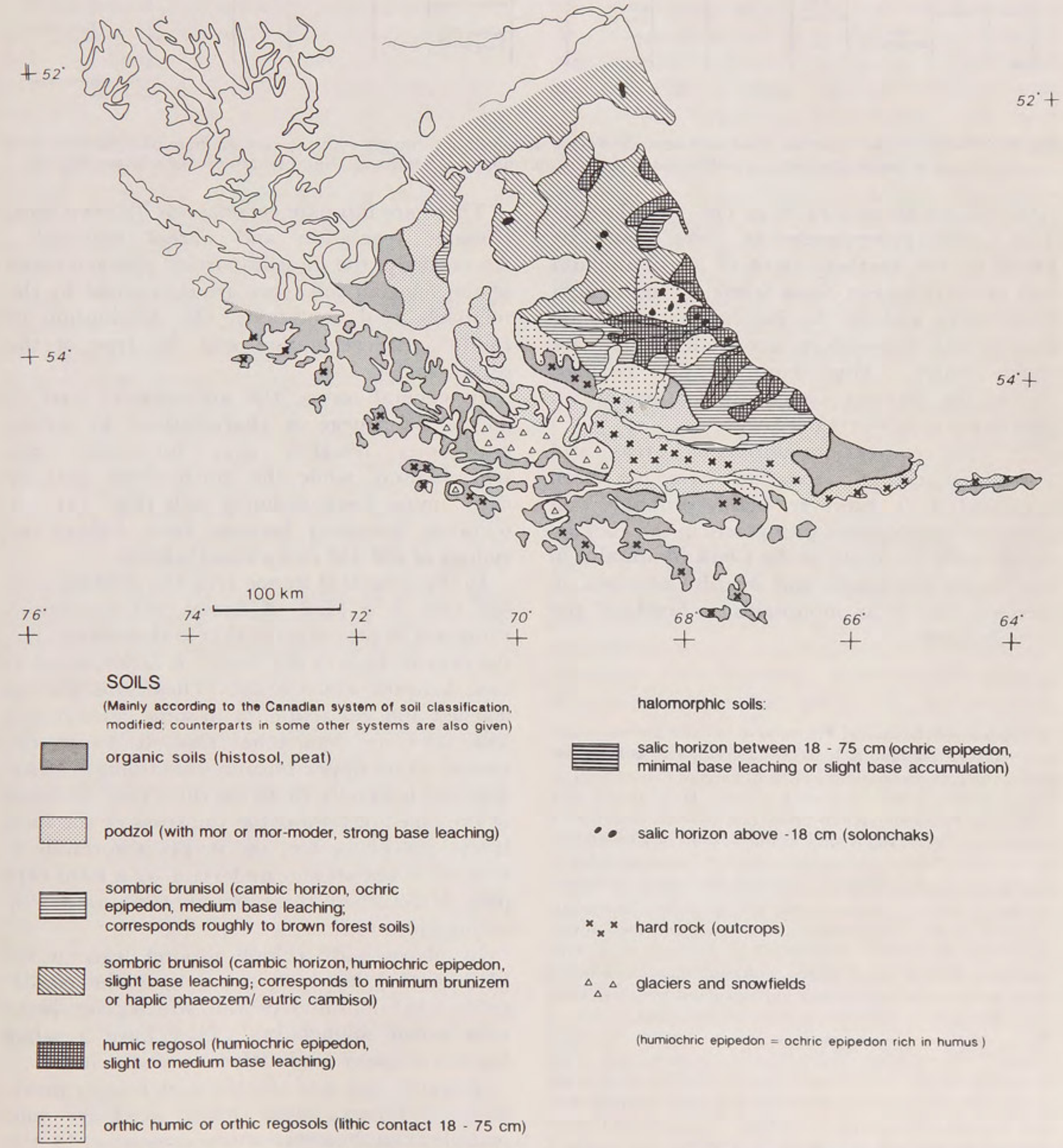

Fig. 16. Distribution of soil types in Tierra del Fuego. Generalized and modified version of Frederiksen (1988: plate 3) soil map, which in turn is based on Landsat interpretations and field observations. Due to the paucity of field observations in the western part of the main island, Frederiksen's map have some obvious misinterpretations, here an attempt was made to correct them on basis of observations made in the present project.

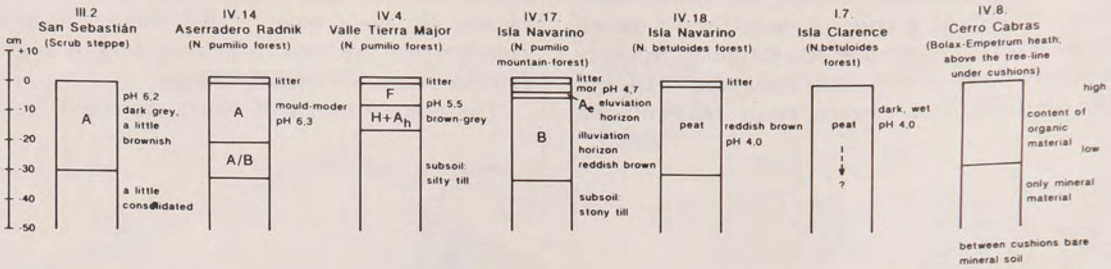

Fig. 17. Profiles of the main soil types in Tierra del Fuego, arranged accordingly with the climatic humidity gradient from brunizem (eutric cambisol) to podsol and to peat soil and mountain heath soil. Numbers refer to the relevees (Fig. 45).

America are not as oceanic as Tierra del Fuego. The closest correspondences there would be found on the southern coast of Newfoundland and in northeastern Nova Scotia, in soutwestern Kamchatka and on the Kuriles, but there are considerable differences; above all, winters are much colder. High humidity and coolness during the growing season are features which they share with Tierra del Fuego.

In this context mountainous areas and altitudinal climatic zonation have not been discussed. It is, however, highly probable that good correspondences with places in the Fuegian sierra could be found at the Coast Mountains in the Alaska Panhandle and British Columbia, in western Norwegian mountains, in Scotland and New Zealand.

4. Soils

The soils of Tierra del Fuego have become known relatively recently. Milano & Marocca (1954), gave, as far as we know, the firts profile descriptions of fuegian soils. Crotti de Ubeda Molina (1955) dealt with podsolic Fuegian soils with petrologic characterization. Holdgate (1961a) described a few soil profiles on Isla Navarino and on some other islands in the western Chilean archipelago north of Tierra del Fuego. Díaz & al. (1960) published a study of soils of most significance for farming. Etcheveherre (1972) gave a schematic overview of the most important soil types and their distribution, mainly from the central and northeastern parts of the Argentine side of Isla Grande. Pisano (1977a) presented a good summary of the various soil types and their variation with site factors in different parts of the Chilean side of Tierra del Fuego, but he gave no concrete descriptions of soil profiles. The hitherto most substancial contribution to the knowledge of the Fuegian soils was provided by Frederiksen (1988), who depicted the distribution of soils at family level and described 35 soil profiles in detail. Bockheim & Ugolini (1990) reviewed the pedogenic zonation in the southern circumpolar region. The following presentation is based on the sources mentioned above as well as the observations made in the present project.

There are intimate correlations between soils, climate, vegetation and parent material. Accordingly, the most important characteristics of the Fuegian soil types are deermined by the relatively cool conditions, the distribution of rainfall, the vegetation and the type of the substrate (Fig. 16).

In general terms, the southwestern part of Tierra del Fuego is characterized by strong tendencies towards peat formation and podzolisation, while the northeastern part by drier, more freely-draining soils (Fig. 17). A tentative boundary between these follows the isohyet of 400-450 mm annual rainfall.

In the semi-arid steppe area the predominant soil type is a kind of brown soil (minimum brunizem or prairie soil), akin to chernozem, but the organic layer is shallower. It is developed in loess beneath which is till. These soils are less leached and less acidic, or in some cases even a little alcaline than other soils of Tierra del Fuego. The upper horizon containing organic material is usually 20-40 cm thick (the thickness of the eipedon follows the thickness of the loess layer), greyish brown, and its pH is normally 6-6.7. It is not seldom underlain by a hard clay pan. If disturbed, these soils are easily eroded by strong, dry winds.

In places with a high ground water table (depressions, low-lying areas near the coast) saline conditions may prevail, which gives rise to soils called solonchaks. They have a saline horizon at the ground surface or near to it.

Towards west and south the increasing precipitation brings about more leaching, and podsolisation becomes more evident. In the deciduous forest and woodland zone with glacial substrate and undulation or hilly terrain the soils are more leached, acidic and are usually relatively well drained. Probably because of abundant leaf-litter the organic horizon is very often of moder-type (pH 4.5-5.5), i.e. the soil type can be characterized as acidic brown forest soils (sombric brunisol with medium base leaching).

If the drainage is poor, the soils develop into gley-podsols. Because of an impermeable clay pan the upper soil layers are saturated with water. The upper horizon is peaty with a very high organic content. On these soils *Sphagnum* bogs can often develop.

In regions with higher precipitation, acidic brown forest soils and podzols develop if the drainage, due to the relief and the substrate, is sufficiently good.

As a consequence of extremely humid and oceanic climate with very high precipitation and isothermal temperature regime in the southwest, the humification process is very slow, and thus deep accumulations of organic material, peat, develop. These peat accumulations are very extensive, covering almost all parts of the terrain and supporting a so-called moorland vegetation.

At high altitudes the frost-weathering produces accumulations of rock debris, from coarse sand to large fragments, and accordingly the soils are lithosols, with very low organic content. In alluviums these kinds of azonal soils contain more humus in the eipedon, and so they constitute humic regosols and rankers.

5. Human impact on flora and vegetation

Tierra del Fuego was populated by four indigenous Indian groups, i.e. Yaghan, Alacaluf, Haush and Ona (Holmberg 1906, Furlong 1917a, b, Lothrop 1928, E. Bridges 1948, 1952, Holdgate 1961c, Goodall 1979). Gusinde (1931, 1937) call Ona and Haush "Selk'man", Yaghan "Yamana" and Alacaluf "Halakwulup". The two latter groups are called terrestrial or foot Indians who arrived to the northern Fuegian steppes about 7.500 years ago (Bird 1938, Laming-Emperaire et al: (1972)*. The former two, i.e. the channel Indians, came to western Fuegian considerably later. Yaghan (south of Península Brecknock) and Alacaluf (north of Península Brecknock) were coastal people in the western archipelago depending on seafood **. Traces of their settlement can be seen everywhere by the shores.

They evidently influenced the coastal vegetation by making small clearings and spreading few invading plants (e.g. *Poa annua, Cotula scariosa*). The Ona lived in the steppes and woodlands in a large part of northern and central Isla Grande. After 1880's they were pushed southwards, even to Isla Navarino (Furlong 1917b). The Haush were a small group inhabiting eastern Península Mitre. Ona were hunters depending on the herds of guanaco and the fossorial rodent tuco-tuco while the other groups subsisted on shellfish and seals (Gusinde 1931, Goodall 1979). Unlike most hunter groups the Ona did not use fire to catch animals (e.g. Holmberg 1906, Furlong 1917 a, b, Gusinde 1931). Howerer its use is reported from Patagonia (e.g. Bird 1938, Heusser 1987b).

The European settlement in Tierra del Fuego was started in the early 1870's by a missionary-anthropologist family at Harberton on the Beagle Channel and at Viamonte on the Atlantic coast (T. Bridges 1892, Martinić 1973, Goodall 1979, Canclini 1986). There was an older settlement around Punta Arenas (at that time also called Sandy Point or Town of Magellan) from where sheep herders started to move to the Porvenir (or Puerto Porvenir)-Altos del Boquerón area in the 1880's. The main spread on the Argentine side took place in the steppe from 1890's onwards in the wake of commercial sheep farming. Gold rushes were also further stimuli for the European invasion and the demise of Fuegian Indians (Kranck 1930c, Gusinde 1931, Goodall 1979).

During this century the Indian groups became extinct through introduced diseases, persecution and mixing with Europeans. The rapid shift in the Fuegian population caused a strong change in the land-use pattern. Land was leassed or sold to farmers and taken into intensive commercial use. Tierra del Fuego soon became quite famous for its wool industry, when hundreds of thousands of sheep roamed the northern

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* Really the antiquity of human presence goes back to 10.000 years B.C. accordingly to archaeological prospections carried on at Tres Arroyos, near San Sebastián, where radiocarbonic dates associated to cultural manifestations between 10.280 and 11.880 years B.P. were obtained. (Massone, M. 1987. *Ans. Inst. Pat.*, Ser. Cs. Soc. 17: (Editor's note).

** The presence the ancestrors of canoeing hunters-gathererd goes back to the fourth millenium B.C. (Orquera, L. and E. Piana. 1987. *Quaternary of South America and Antarctic Peninsula.* 5. Rotterdam. (Editor's note).

grasslands.

The peak of the rural Fuegian population was reached after the World War II when ranches and sawmills were established into the most remote places of the archipelago (Butland 1957)*. Since then many of them have been abandoned as the mainstream of the economy moved to the towns. Most of the forested area of Tierra del Fuego still remains in the possession of the government. Exploitation is based on concessions. Lately the tax free Argentine side attracted multinational industry, growing immigration and summer tourism causing social and environmental threats both in Ushuaia and Río Grande. Recently the cancellation of tax-free adventage has had a negative impact on the economy of Ushuaia.

For some decades there were two distinct European settlement patterns in Tierra de Fuego. The main population concentred on the northern grasslands, especially around Porvenir. The average farm size on the Argentine side was much larger compared to the Chilean side. Thus there were relatively many peasant farmers in the Chilean Fuegia. Large Argentine private farms made Río Grande a considerable commercial centre for the wool industry. From the main Magellan port Punta Arenas, there was some movement into the channels and islands of the misty and forested Chilean archipelago by small-scale farmers. Today only the settlement of northern Isla Navarino is conspicuous. In addition to sheep or cattle the islanders' economy relied on fisheries and forestry. (Butland 1957).

The spread of the European settlement has led to considerable transformations of the Fuegian biotopes and formation of new habitats. Ruiz-Leal (1954) noted the spread of *Çerastium fontanum, Capsella bursa-pastoris, Chrysanthemum leucanthemum* and *Bellis perennis* in the surroundings of Ushuaia. Moore & Goodall (1977) and Moore (1983a) list the Fuegian adventive flora (about 120 species). Brion et al. (1988) found 43 alien vascular plants from the forests of Argentine Fuegia. In a larger scope the problem of native and introduced vegetation has been discussed by Philippi (1886), Hauman (1928), Heim (1928) and Eriksen (1972). A recent thorough presentation edited by Solbrig (1984) concers the human impact on Andean ecosystems. Spegazzini (1910, 1911), Davies (1940), Parodi (1945), Roseveare (1948), Ragonese (1967), Serra (1970) and Duga (1980) discussed the vegetation of southern South America from the forestry, agriculture or animal husbandry points of view.

The clearing of forests from coastal areas has made open friges around Isla Grande and northern Isla Navarino. Commonly whole mountain sides were cleared to make access to the meadows and grasslands above timber line. Owing to a layer of organic peat, erosion is often avoided but the replacement pasture consists of coarse seepage tolerant graminoids and ground herbs of swampy conditions. At higher altitudes clearings increased the dominance of wind-tolerant heathland plants, especially those of the cushion form (*Polytricum, Bolax, Drapetes, Empetrum*). In grazed clearings the establishment of *Nothofagus* is greatly reduced, and natural regeneration even without grazers takes apparently several decades (McQueen 1976).

In drier lowland areas (e.g. northern Península Mitre) some wide, burned areas are found with grasslands consisting of indigenous forest species (e.g. *Acaena* spp., Moore 1983b, Fig. 18). Their quick overgrowing by *Nothofagus pumilio* is anticipated, if both grazing and fire are removed. Woodland ridges near settlements have been frequently cleared for firewood. Without grazing these would slowly regenerate but in the ecotonal areas, e.g. east of Río Grande town, the advancement of steppe including *Empetrum* and introduced pasture plants has taken place (Serra 1970, McQueen 1976).

Outdoor agriculture is practically non-existent in Tierra del Fuego as only potatoes and a few garden crops (carrot, cabbage, lettuce, strawberry) may survive in sheltered locations. The general harshness of the cool summers prevents the production of reasonable crops (Parodi 1964, Goodall 1979, Weischet 1985). Some oats and barley are cultivated for green fodder for cattle but with limited success.

The Fuegian steppe has two strong indigenous constituents: *Chiliotrichum difusum*, an

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* This process was also notorious at the Chilean part of the island and was mainly based on the development of oil prospection and explotaition, since 1945, and in the agrarian recolonization and subdivision following the recuperation of fiscal lands previously leassed to large sheep companies, mostly between 1940-1945. (Martinić, M. 1982. *La tierra de los Fuegos.* Punta Arenas). (Editor's note).

19.

Fig. 18. Extensive area burned over a couple of years ago in northern Península Mitre. Photo: Sakari Tuhkanen (1987).

Asteraceous shrub, and *Festuca gracillima*, a tussock grass. These dominate over wide distances in the dry northern Fuegia forming independent stands or joint mosaic communities, preforming well under grazzing conditions with European introductions (Serra 1970). The assumed vegetational changes in a hundred years time have been relatively small compared to more northerly grasslands. Between the tall *Festuca* tussocks various other indigenous grasses and herbs have held their position. The sheep feed well on natural Fuegian grasslands, however, overgrazing leads quickly through phase of rosette (*Tarazacum*) and creeping (*Cotula*) herbs to heathland forms with dominating cushion plants (*Bolax-Empetrum* communities) (McQueen 1976).

Taraxacum officinale (s. lat.), *Cerastium fontanum* and *Poa pratensis* are the most widely spread Northern Hemisphere plants in Fuegia. The former is locally dominating, especially in clearings. *Rumex acetosella* spreads along roadsides and benefits from trampling and overgrazing, but it is less frequent than in northern Patagonia (Davies 1940). *Medicago sativa* and *Dactylis glomerata* sown on special plots seem to be the only active introductions. The latter may even run wild.

The clearing of sparsely wooded ridges south of Río Grande town have pushed the tree-line somewhat southeastwards. The marginal woodlands seem to degenerate, because sheep and guanacos eat the regenerative shoots and the few seedlings. The regression of marginal woodlands was thought to be primarily climatic by Auer (1933a) and E. Kalela (1941a) but this is questionable (Veblen & Lorentz 1988, Veblen & Markgraf 1988). On the Altos del Boquerón the unique *Drimys winteri-Maytenus magellanica* woodland has been almost completely destroyed by collection of firewood and bush fires that are drawn by the wind across entire hillsides. Slow-growing and hard-wooded *Maytenus magellanica* has disappeared from many places for fuel and carpentry (Alonso 1942). Because of decorative value *Drimys* may, on the contrary, have been preserved. The intention to make pastures on Boquerón has led to the aggresive spread of *Chiliotrichum* scrub that has an advantage on randomly sown foreign grass seed (*Dactylis-glomerata, Anthoxanthum odoratum, Trifolium* spp.).

The clearing of closed forests or woodlands for desired grasslands has not been successful in Tierra del Fuego. The spontaneous outcome is the spread of forest floor or mountain meadow species (McQueen 1976, Moore 1983b). *Poa pratensis* seems to be important in Fuegia for its ability to quickly fill open eroded or overgrazed spots. In general broad-leaved northern pasture grasses (e.g. *Festuca pratensis, Dactylis glomerata*) seem to tolerate badly the dry and windy Fuegian summers.

Cattle are generally kept primarily for commercial reasons in Tierra del Fuego. Along Seno Almirantazgo and the Beagle Channel large deciduous-evergreen forests have been cleared for cattle pastures. Little else is done for the pastures and cattle grazing favours quickly establishing European species (*Poa pratensis, Poa annua, Cerastium fontanum*) on welldrained sites. On seepage sites with humic soils, meagre communities with indigenous Cyperaçeae and Juncaceae are formed.

In the southern Andes (south of 45° S) *Nothofagus pumilio* is the most important forestry tree. Because it has no exceptional qualities the southern forests have not so far been exploited to a great extent. In Tierra del Fuego several sawmills have operated on both flanks of the Marginal Cordillera. The wood extraction has been unplanned, random and exploitative concentrating on the areas of best growth (the Lago Fagnano-Seno Almirantazgo area). However, both *Nothofagus pumilio* and *N. betuloides* in mixed stands are very good in regenerating on small clearings inside the forest (as happens in natural succession, McQueen 1976). A larger part of the central Fuegian forests especially in the mountains are still in their original primeval state. The archipelagic forests of *Nothofagus betuloides* have remained practically free of human impact. Near anchorages forest patches or scrub may have been destroued for fuel or construction wood.

Tierra del Fuego is not an unimportant summer resort in Argentina which may lead to some environmental problems in the future. There is a large national park with varying landscapes in Lapataia west of Ushuaia to conserve various natural communities of central Tierra del Fuego for tourism and reserach (Correa Luna 1964). Drilling of oil has also created a new hazard to the Fuegian nature.

6. The impact of native and introduced fauna on the Fuegian environment

The Fuegian forest fauna is not large, but some of the animals have profound effects on the vegetation. The guanaco (*Lama guanicoe*) is by far the most important. It is very common everywhere in forested areas of Isla Grande and to a less extent on Isla Navarino (Gusinde 1931, Goodall 1979). The guanaco is both a grazer in open communities and a browser of *Nothofagus* where the field layer in Fuegian forests is scarce (McQueen 1976). While controlling the under growth it is also a good distributor of both forest, steppe and moorland flora. The central Fuegian grazing grounds lie mostly above the tree line where guanacos spend much of their time enhancing exchange of diaspores between open altitudinal and closed forest communities. During winter grazing guanacos depend on coarse graminoids of the lowland bogs (Gusinde 1931). The spread of some adventivous herbs (*Stellaria media, Cerastium fontanum, Poa annua, Poa pratensis*) all over Isla Grande is attributable to guanacos. They distribute also many indigenous species with attaching diasporas (notably *Osmorhiza* spp., *Acaena* spp., *Galium* spp. and most grasses, J.L. Lanata 1985, pers. comm.).

The North American beaver (*Castor canadensis*) and muskrat (*Ondatra zibethica*) were introduced in 1946 as fur animals into the Fuegian inland waters (Correa Luna 1964, Goodall 1979). Without enemies other than man, beaver populations have increased and spread to practically all forested watersheds on at least Isla Grande and Isla Navarino. By flooding the rivers and brooks they have caused a strong paludifying effect (Sielfeld & Venegas 1980, Manconi & Balabusic 1980). Dense populations mix the water into dystrophic brown by liquifaing humic acids. Often beavers extend the size of overgrowing valley fens by blocking the outlets. In the area of gallery forests in lowland Peninsula Mitre beavers have locally eradicated allmost all woody growth.

The European rabbit (*Oryctolagus cuniculus*) has also spread extensively, which has favoured grazing-tolerant species (e.g. *Poa annua, Cotula scariosa, Pratia repens*) in places where its population is dense. Trampling of sheep and the competition of rabbit has greatly decreased the numbers of the indigenous rodent, tuco-tuco

(*Ctenomys magellanicus*) (Gusinde 1931, Goodall 1979)*

III. THE FUEGIAN FLORA AND VEGETATION

1. *Flora*

Floristically southern South America has been a controversial area between the Antarctic and Neotropical floristic kingdoms. In the earliest outlining Schouw (1822) included Patagonia, Fuegia and the Falkland into the Antarctic kingdom. Diels (1908) proposed a division of a western mountainous part (to the Antarctic kingdom) and eastern plains of Patagonia and Tierra del Fuego (to the Neotropical kingdom). The Pacific side of southern South America has commonly been referred as the Magellanic floristic province of the Antarctic while the Atlantic side has been named either the Patagonian, Fuegian-Flaklandic or South Patagonian-Falklandic provinces of the Neotropics. Good (1947) placed all southern South America into a single Patagonian floristic province within the Antarctic kingdom. Huschel (1963) and Knox (1963) proposed their own neoaustral kingdom corresponding with Good's Patagonian area. Mattick (1964) refined Diels' system by delimiting the two kingdoms in southeastern Patagonia along the semi-desert-steppe boundary leaving all Fuegia to the Antarctic kingdom. Regarding the actual geographical delimitations great variations abound. The main regionalizations are assembled by van Balgooy (1971).

In southeastern Patagonia and northern Tierra del Fuego the Antarctic floristic element of moist and cool conditions (e.g. cushion plants, soft herbs) is mixed with the Patagonian semi-desert flora (e.g. spiny dwarf shrubs, tussock and annual grasses) in a transitional belt called tussock steppe (Davies 1940), the marginal Patagonia (Frenguelli 1941), humid steppe (Beetle 1943) or the Subandean region (Cabrera 1978). Several typically Antarctic genera (e.g. *Acaena, Cotula*) are conspicuous in this transitional belt because of higher humidity compared to more northern parts of eastern Patagonia. Quite an amount of local endemism is found in the Magellanic region (e.g. Donat 1935b, Correa 1969-1988, Moore 1983a).

The Antarctic genera represent the ancient Gondwana flora. Their range cover southwestern South America, New Zealand, Tasmania and New Caledonia with extensions along the Andean and Indo-Malayan mountains chains (e.g. Du Rietz 1940, Skottsberg 1960, Bader 1960, Troll 1960, van Steenis 1972, Troll & Lauer 1978). These groups are called "Palaeoantarctic" by Skottsberg (1960) and continental "Antarctic" by Wace (1965). There is additonal fossil evidence of their wider previous area from for example Kerguelen and the Antarctic Peninsula (e.g. Florin 1940, Couper 1960). They include older (Tertiary) groups of vascular plants that evolved before the breaking of the West Antarctic land bridges (e.g. Brundin 1966, 1970, van Zinderen Bakker 1970, Keast 1971). In the belt of continuous westerly winds (40-60° S), recent (Quaternary) spreading of some thirty cool oceanic or Subantarctic herbs and grasses (Greene & Greene 1963, Greene & Walton 1975), i.e. the maritime Antarctic element of Wace (1965), has taken place. This includes especially wind-tolerant cushion-forming vascular plants but also hygrophytes and tall tussock grasses (Godley 1960a, 1967, 1978, Wace 1965).

The Antarctic element is characterized by the dominance of the evergreen habit that is still preserved in the Australasian area as most of it falls within temperate or subtropical climates. In southwestern South America the Antarctic element gradually adapted to very cool and windy but almost frostless conditions. The climatic severity has also led to the evolution of the deciduous habit (and the invasion of continental interior areas) e.g. within the genus *Nothofagus* that is predominantly an evergreen genus elsewhere. The alternation of physiognomically tundra-reminescent landscapes (vascular cushion plant bogs) with rain forest growth forms in a cool, wet and windy climate has led to varying interpretations of the phytogeographical position of the Fuegian vegetation (e.g. Pérez-Moreau 1944, Pérez-Moreau & Sgrosso 1949, Bliss 1979, Tuhkanen in press).

The majority of the conspicuous Magellanic genera show Antarctic or Southern Hemispheric affinities, e.g. *Abrotanella, Acaena, Azorella, Carpha, Colobanthus, Cotula, Discaria, Donatia, Drapetes, Embothrium, Fuchsia, Gaul-*

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* The "pampa fox (*Canis griseus*) was introduced in the 1940's as a possible predator on the European rabbitt. (Editor's note).

theria, Gunnera, Hebe, Luzuriaga, Marsippospermum, Nothofagus, Oreobolus, Rostkovia and *Uncinia* (Good 1933).

Recently spread insular circumantarctic flora includes e.g. *Acaena magellanica, Colobanthus* spp., *Callitriche antarctica, Ranunculus biternatus, Agrostis magellanica, Blechnum penna-marina, Lycopodium* spp., and *Azorella selago* (Greene & Walton 1975).

The Neotropical element is seen in the dryland vegetation in the abundance of genera like *Senecio, Adesmia, Leucheria, Frankenia* and *Verbena* (especially shrubs, dwarf shrubs and semi-wooded herbs). There is conspicuous endemism in *Nassauvia, Mulinum* and *Nardophyllum* (Good 1933). The xeric growth forms are most evident as in semi-desert areas but the species of Patagonian affinity have commonly evergreen microphyllous imbricate or convolute leaves.

There are a number of bipolar plants in the Fuegian flora which have spread either along the Rocky Mountain-Andean route or the Australasian-Antarctic route (Du Rietz 1940, 1960, van Steenis 1972). Some of these migrations are relatively young (Tertiary) and we have in the Magellanic both bipolar species as well as close southern counterparts of boreal species. The bipolar elements is substantial among alpine, meadow, aquatic and fenland vascular plants and in mosses and lichens. The bipolar vascular genera include e.g. *Adenocaulon, Alopecurus, Antennaria, Berberis, Chrysosplenium, Draba, Empetrum, Osmorhiza, Primula, Phleum, Ribes, Saxifraga* and *Trisetum* (Good 1933).

a. Vascular plants

The firts cornerstones of the knowledge of the Fuegian vascular flora were established by the exploring expeditions in the 18th and 19th century. These include Forster & Forster (1976), de Jussieu (1789, Commerson's material), Forster (1789), Hooker & Arnott (1835-1841, including Eights' material), W.J. Hooker (1844, J.D. Hooker's material), Hooker (1847, including Menzies', King's and Darwin's material), Hombron & Jacquinot (1852), Decaisne (1853, Hombron's and Jacquinot's material), Brackeridge (1854), Gray (1854, Wilkes' material) and Britten (1905, Banks' and Solander's material).

Between about 1850 and 1910 various international scientific expeditions explored Tierra del Fuego contributing major mainly floristic works by Grisebach (1856, Lechler's material), Lechler (1857), Cunningham (1871b), Tizard et al. (1885), Engler (1889, Naumann's material), Franchet (1889, including Savatier's material), Spegazzini (1896), Alboff (1896, 1902), Alboff & Kurtz (1896), Dusén (1900), de Wildeman (1905), and Skottsberg (1905a, 1906b). Minor contributions on Fuegia include works by Schultz-Bipontinus (1855), Hariot (1884, 1900), Palacky (1884), de Amezaga (1885), Hackel (1885), Safford (1888 a,b), Kurtz (1902), Autran (1905), Schenk (1905), Skottsberg (1906a), Dusén & Neger (1908) and Stapf (1909). Works on southern and western Patagonia by Ball (1886, 1891), Spegazzini (1897 plus numerous addenda between 1896-1911 to his earlier monographs) and Dusén (1901, 1907b) are also relevant for Fuegia.

A comprehensive flora was initiated by Reiche (1896-1911) who published the flora of Chile in six volumes. The extratropical South American Cyperaceae were listed by Kükenthal (1899). The first Flora Patagonica included contributions on ferns by Macloskie & Underwood (1903) and seed plants by Macloskie (1903-06). Subsequently a revision of the flora was published by Macloskie, Dusén & Skottsberg (1914). Schröter and Hauri (1914) presented a synopsis of the vascular cushion plants.

Relative inactivity within floristic studies in Tierra del Fuego followed the completation of the Chilean and Patagonian floras (Skottsberg 1926, Roivainen 1936, Martín 1949, Ruiz-Leal 1954). Skottsberg (1924), Roivainen (1933a, b) and Kalela (1940) dealt with southern Patagonia. The majority of later works relating to the flora of Tierra del Fuego focused on special systematic or morphological groups (e.g. Hill 1918, Hauman 1919, Looser 1932, 1948, 1961-62, Langdon 1947, Rauh 1949, Kausel 1949, Diem & de Liechtenstein 1959, Faden & Weinberg 1962, Grondona 1964, Pyykkö 1968, Walton 1979). Muñoz (1966) made a revision of the Chilean flora.

After producing a recent flora of the Falkland Islands D.M. Moore (1968) carried on the tradition of floristic work (Moore 1974, 1975,1983c, Moore et al. 1970, Moore & Chater 1971, Moore & Doggett 1975, 1976, Moore & Goodall 1977) which resulted in a meritorous Flora of Tierra del Fuego (Moore 1983a). There have been few major works on the flora of both Argentine and Chilean Patagonia in the recent decades, but the progress has been reflected in the new Flora Patagónica edited by Correa (1969-88). Important contributions have recently been published on the outlying islands; on Islas Diego Ramírez by Aubert de la Rüe (1959, Pisano y Schlatter (1981b), on Isla Noir (Pisano & Venegas 1984) and on Staaten Island by Dudley (1981) and Dudley & Crow (1983). Godley (1964) and Pisano (1970, 1983b, 1985-86, 1987) give accounts on the South Patagonian fiordland.

Palaeoantarctic flora connections were already noted by Hooker (1847). The Tertiary fossil records and the question of the common Antarctic biota has since then been pondered by Hedley (1891, 1912), von Ihering (1891), Ortmann (1901), Dusén (1907a), Halle (1913), Rodway (1915), Skottsberg (1915,1939,1953,1955), Hicken (1921), Hill (1929), Andrews (1940), Copeland (1940),Florin (1940), Gordon (1949), Camp (1952), Turrill (1953), Dawson (1958), Couper (1960), Du Rietz (1960), Darlington (1960, 1965), Holdgate (1961b), Cranwell (1963) and Schmithüsen (1964). von Ihering (1893), Good (1947) and van Balgooy (1971) have discussed widely the essences of the southern floristic kingdoms.

After Wegener's theory of continental drift received support from plate tectonics (cf. e.g. Adie 1963), the relationships between southern biota have been treated by Brundin (1965, 1966, 1970), Godley (1967), van Zinderen Bakker (1967, 1970), Darlington (1970), Gressitt (1970), van Balgooy (1971), Keast (1971), O'Brian (1971), van Steenis (1972), Moore (1972, 1980), de Moral (1978), various authors in Troll & Lauer (1978) and Humphries (1985).

Bipolar connections of the southern South American biota have been treated by Philippi (1892), Kurtz (1899), Delpino (1900), Hackel (1906), Petitmengin (1907), Heintze (1918), Good (1933), Du Rietz (1940, 1960), Moore & Chater (1971), Moore (1972, 1983a, c), Moore et al. (1972) and Schwaar (1980). Circumantarctic insular biogeography has been reviewed by Schenk (1905), Skottsberg (1905b), Rudmose Brown (1928), Vallaux (1929), Lindsay (1940), Deacon (1960), Skottsberg (1960), Wace (1960, 1965), Knox (1963), Kuschel (19637, Thorne (1963) and Greene (1964). Checklists of insular Subantarctic vascular plants have been gieven by Greene & Greene (1963) and Greene & Walton (1975).

Regional floristic and biogeographical reviews treating southern South America have been presented by Ball (1887, 1891), Neger (1901), Skottsberg (1904), Hauman-Merck (1916) Seckt (1919, 1943), Hauman (1931), Skottsberg (1932), Donat (1931, 1932, 1934, 1935a), Looser (1932, 1948), Ragonese (1936), Frenguelli (1941), Beetle (1943), Parodi (1945), Smith & Johnston (1945), Pérez-Moreau (1944, 1945), Vellard (1948), Fuenzalida (1950), Cabrera (1953, 1958, 1971, 1978), Soriano (1956), Aubert de la Rüe (1959b) and Pisano (1972b, 1973, 1975, 1980, 1983a). General biogeography has been dealt by Kuschel (1960). Mann (1960) and Kuschevich (19747 while Pisano (1975) gives a more specific treatment on the Magellanic area. The affinities of the Fuego-Patagonian flora have been dealt by Macloskic (1906), Good (1933), Wace (1965), Godley (1967), Moore (1972, 1980, 1983a, c) and Pisano (1984).

Castellanos & Pérez-Moreau (1941) compiled a concise, regionally arranged bibliography of the Argentine botany up to that time. Dudley & Crow (1983) provide one of the most complete recent bibliographies on the Fuegian flora and vegetation, though regrettably, its value is decreased by numerous errors. Moore (1983a) presents a very reliable bibliography but that of Arnaud et al. (1967) is faulted by errors.

Number of species. In total there are records of about 570 vascular plants growing in Tierra del Fuego of which ca. 430 are considered native (Moore & Goodall 1977, Moore 1983a, Brion et al. 1988). Moore applied a broad species concept in his flora accepting wide morphological variation for taxa inhabiting broad ecological ranges. The species number for Fuegia in the yet uncompleted Argentine Flora Patagónica (Correa 1969-88) will be higher due to a narrower species concept. According to Moore (1983a), 28 ferns, 2 gymnosperms, ca. 270 dicotyledoneous and ca. 120 monocotyledoneous plants are found in Tierra del Fuego their relative shares being comparable to the boreal areas. There are only three forest forming trees, six additional subcanopial or secondary trees, 12 shrubs, 25 dwarf shrubs, 26 cushion plants, 86 graminoids, 25 annuals, six epiphytes, 27 aquatic plants (Moore 1983a).

Growth forms. The number of trees in Tierra del Fuego is low. Two deciduous southern beeches (*Nothofagus antarctica, N. pumilio*) form the wide central Fuegian forest island landscape and its closed forests. The latter reminds in general structure of the temperate West European *Fagus* beechwoods. The evergreen Pacific forests are more varied with the usual *Nothofagus betuloides* underlain by both secondary trees (*Drimys winteri, Maytenus magellanica*) and tall scrub (e.g. *Berberis ilicifolia*). The conifers are lacking except for one oceanic moorland species (*Pilgerodendron*)*. This structure has best analogies in New Zealand and Tasmanian mountain forests.

There are two deciduous shrub species (*Ribes magellanicum* and *Berberis buxifolia*) in Tierra del Fuego. They are characteristic for the interior of Fuegia and for mountain forests. The rest are evergreen and their number and coverage increase towards both western evergreen forests and the northern steppes. At high altitudes or over seaward cliffs most Fuegian trees may transform into scrub and mix with the true shrubs (*Berberis ilicifolia, Pernettya mucronata, Escallonia serrata, Desfontainia spinosa*). Also steppe shrubs may mingle into extensive mixed scrubs (*Chiliotrichum diffusum, Lepidophyllum cupressiforme, Baccharis* spp., *Senecio* spp., *Perezia recurvata*). Besides tall shrubs woody *Empetrum rubrum, Maytenus disticha, Pernettya antarctica,* and semi-woody (*Pernettya pumila, Drapetes muscosus, Senecio* spp.) dwarf shrubs are common in various communities. Some of the oceanic dwarf shrubs (*Lebetanthus myrsinites, Philesia magellanica*) are climbers covering the tree trunks.

Ferns are important constituents in the Fuegian flora, the majority of them are evergreen and inhabit the moister side of the archipelago. These often have creeping rhizome (*Asplenium dareoides, Blechnum pennamarina, Gleichenia quadripartita*) that help their spread. Several *Hymenophyllum* species and various bryophytes contribute to the characteristic double ground layer of evergreen woods. Some ferns (*Serpyllopsis caespitosa, Hymenophyllum secundum, Grammitis magellanica*) are epiphytic on trunks.

* And one shrubby prostrate species (*Dacrydium fonckii*) found only at Hoste island. (Editor's note).

Megaphyllous ferns include *Cystopteris fragilis* in dry forests, *Polystichum multifidum* in deciduous-evergreen forests and *Blechnum magellanicum* of rosette tree form in oceanic moorland.

The number of hard or lax cushion forming plants is high in Tierra del Fuego. They derive from many different families (e.g. Apiaceae, Asteraceae, Donatiaceae, Stylidiacear, Iridaceae, Cyperaceae) and have adapted to open and windy Fuegian environments. In the outer Pacific fringe *Donatia fascicularis, Oreobolus obtusangulus, Astelia pumila* and *Drosera uniflora* are the main constituents of the lowland vegetation (moorland). Convex hill tops and windy seabanks in dry northern Isla Grande have their own drought adapted selection of cushion plants. Under windy and sheltered conditions some plants may develop into lax or cushion form (*Drapetes muscosus, Lycopodium magellanicum, Saxifraga magellanica, Nassauvia* spp., *Caltha* spp., *Colobanthus* spp.). Above an altitude of 500-700 m the mountain slopes are covered with a cushion heah mosaic (*Azorella lycopodioides, A. selago, Bolax gummifera, Abrotanella emarginata*) stabilizing the ground for other vascular plants to root. Higher up mass-movement processes such as soil creep and rockslides break these cushion beds.

Graminoids have but few broad-leaved rhizomatous species in closed communities *(Bromus, Trisetum, Agrostis)*. In open forests islands small *Festuca* and *Uncinia*, and introduced *Poa* must be added. In the various steppes and heathland *Agropyron, Alopecurus, Deschampsia, Festuca, Hordeum, Luzula, Poa* and *Trisetum* are characteristic. In mountain grasslands *Agrostis, Festuca, Luzula, Phleum, Poa* and *Stipa* are found. In wetlands *Agrostis, Alopecurus, Anthoxanthum, Calamagrostis, Carex, Cortaderia, Deschampsia, Juncus, Marsippospermum, Poa, Rostkovia* and *Schoenus* are conspicuous graminoid genera. The tussock form has evolved in *Calamagrostis (Deyuxia), Deschampsia, Festuca, Poa, Schoenus, Stipa* and *Uncinia*.

Distribution and affinites. A large part of native Fuegian species share a small total area south of 51°-52° S where the transition from steppe to semi-desert conditions takes place in the east. Several Fuegian species of neotropical affinity extend northwards either along the narrow steppe-corridor in the eastern Andean foothills or along the Atlantic coast. A few reach the northwestern Argentina or southeastern Brazil (Good 1933, Moore 1983a). Accordingly species of the Pataognian semi-desert are infrequent even in driest Tierra del Fuego (Correa 1969-88, Cabrera 1978, Soriano et al. 1983).

On the Pacific margin of the Andes the ocean suppresses the north-south climatic gradient and characteristic western Fuegian species cover often the whole area of dominant *Nothofagus betuloides-N. pumilio* forests till about Golfo de Penas at 46-48° S. This is the limit between the (southern) Magellanic and (central Chilean) Valdivian coastal forest as proposed by e g. Hauman-Merck (1916), Skottsberg (1931a), Pérez-Moreau (1944) and Quintanilla (1981). In montane forests some species reach 34° S in the company of *Nothofagus pumilio* (Schmithüsen 1956, Moore 1983a). The western Fuegian flora has also a considerable affinity to the peaks of Másafuera (Skottsberg 1925, 1931b). Several species of wetland communities extend their ranges into northern Chile and Perú, quite a few have disjunct ranges in the mountains in temperate western United States-Mexico or in the circumboreal zone (Moore 1983a).

Using the data of Moore (1983a), 14% of the Fuegian vascular species have their ranges within southernmost Patagonia (Fig. 19). Half of the Fuegian species do not reach outside Patagonia or beyond about 40° S. Twenty percent extend their ranges to North Chile and the northwestern Argentina. Five percent are found along the Andes in Perú-Ecuador and a couple of species in central América. Eleven percent have a bipolar distribution.

Within the circumantarctic 127 Fuegian species are found on the Falkland Islands and 24 species in South Georgia (Fig. 20). The islands of the Kerguelen floristic province (Skottsberg 1960) share 14 species and the New Zealand shelf islands 10. Nineteen species are found in the New Zealand main islands, Tasmania, Australia, Lord Howe Island or New Guinea. The Gough-Tristan da Cunha and St. Paul-Amsterdam groups possess seven Fuegian species but the African continent only two. In the Chilean Pacific the Juan Fernández Islands share 11 species with Tierra del Fuego but the Desventuradas none at all (Moore 1988a).

Nothofagus species are perhaps the most famous representants of the Antarctic floristic element. The Fuegian *Nothofagus* species are

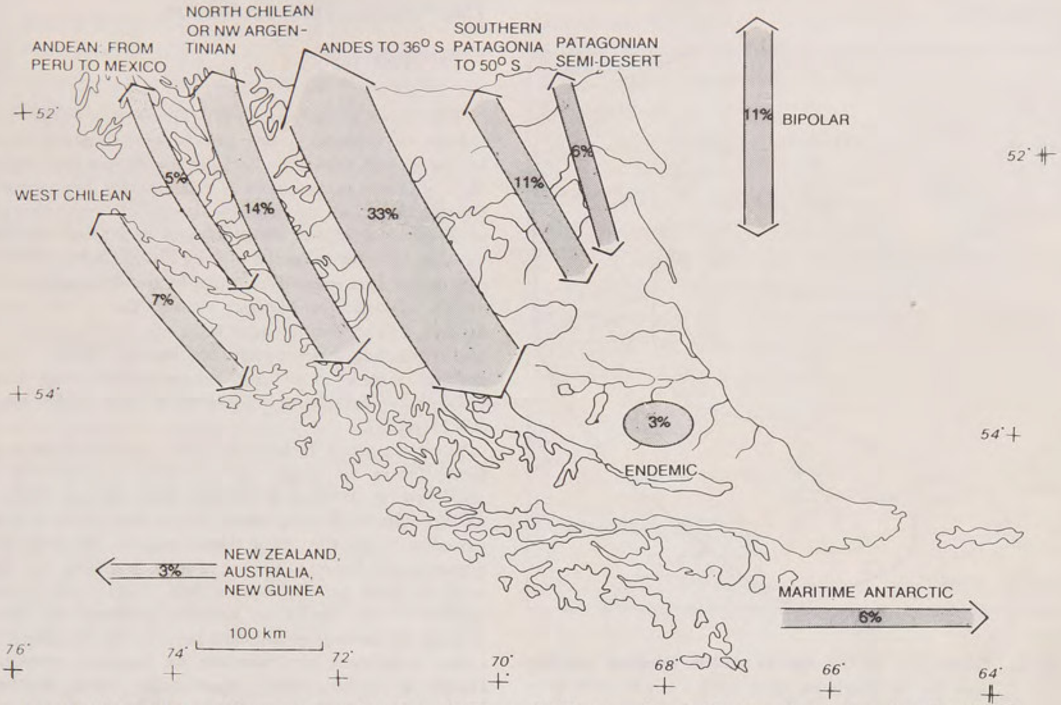

Fig. 19. Affinities of the indigenous vascular flora of Tierra del Fuego. The main directions of species distribution indicated by percentages of the total flora (417 species). The groups, roughly delimited, are as follows: Fuegian endemics, Magellanic endemics to 52-50°S, temperate West Patagonian and Valdivian rain forest from 50°S to about 39°S, Central Cordilleran with a deciduous component from 50°S to about 35°S, steppes and shorelands of the Atlantic side (Patagonia north of 52°S, Pampas, Chaco), sclerophyllous northern half of Chile and Perú to about 15°S, tropical Andes to about 20°N in México, bipolar, maritime islands of the south seas, southern continents (New Zealand, Australia, New Guinea). The regions and their delimitations adapted from Schmithüsen (1956) and Wace (1960); the floristic data extracted from Moore (1983a).

commonly infected by the parasite vascular plant genus *Misodendron* (endemic to South American *Nothofagus*) and the ascomycete *Cyttaria* (specific to *Nothofagus* in general). The other tree genera (*Drimys, Embothrium, Maytenus, Pilgerodendron, Pseudopanax, Tepualia*) also have southern hemispheric distributions (Krüssmann 1972, 1976-78). The Antarctic floristic element showing southern circumantarctic or disjunct Magellanic-New Zealand ranges is best represented in the archipelagic moorland and swamp forests. These communities include shrubs (*Blechnum* sect., *Lomaria, Desfontainia, Escallonia, Fuchsia, Hebe, Gaultheria*), climbers (*Lebetanthus, Luzuriaga*), cushion plants (*Astelia, Azorella, Bolax, Donatia, Oreobolus*) and giant tussock grasses (*Poa*). However, bipolar Hymenophyllaceae constitute the most diverse vascular genera in the areas of highest rainfall. Widely distributed cosmopolitan wetland genera (*Callitriche, Drosera, Montia, Plantago, Ranunculus*) are also conspicuous. *Gleichenia* displays tropical affinity. (Good 1933, Skottsberg 1960, Wace 1960, 1965, Troll 1978, Moore 1983a).

Herbaceous species of bipolar temperate genera (*Adenocaulon, Berberis, Cerastium, Cystopteris, Galium, Osmorhiza, Polystichum, Rubus, Trisetum, Valeriana, Viola*) seem to be some what more characteristic in the well-drained, mainly deciduous forests than southern genera like *Acaena, Cotula, Gavilea, Gunnera, Lagenifera, Maytenus, Schizeilema* and *Uncinia*. Coastal or seral communties include South American shrubs like *Chiliotrichum* and *Chiliophyllum* and southern *Discaria, Embothrium* and *Fuschsia*. (Good 1933, Skottsberg 1960, Troll 1978).

The flora of the Magellanic steppe shows only a limited neotropical affinity in its marginal parts by having rather few dryland shrubs, cushion shrubs, dwarf shrubs and cushion herbs (*Adesmia, Anarthrophyllum, Eriachaenium, Frankenia, Lepidophyllu, Nardophyllum,*

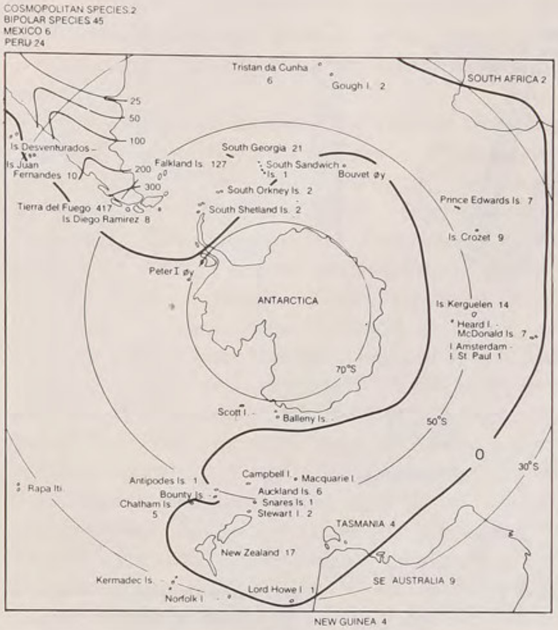

Fig. 20. Occurence of the species of the Fuegian vascular flora in the southern lands with an indicated zero-line. The number of common species declines sharply eastwards after the Falklands Islands and South Georgia. Most of the common circum-antarctic species are probably distributed by sea birds in the westerlies zone. Only Kerguelen and New Zealand, being ancient tracts of Gondwana and largest at the area, have a higher number of Fuegian species. The empty sector in South Pacific is obviously due to the absence of any appropiate land there. Compiled from Moore (1983a).

Perezia). South American *Chiliotrichum Chiliophyllum* and *Mulium* form rather mesic shrublands and extend under forest or woodland. Some prominent members of tussock grasslands (*Acaena, Cortaderia, Cotula*) have a southern affinity. (Good 1933, Godley, 1960, Cabrera 1978, Cleef 1978).

The South American element is quite conspicuous in the windswept fjell areas (*Baccharis, Leucheria, Nassauvia, Senecio*) along southern cushion planta genera (*Abrotanella, Azorella, Bolax, Drapetes*). The lowland heathlands have both bipolar-cosmopolitan (*Agrostis, Antennaria, Deschampsia, Empetrum*) and southern cushion genera. In mires southern *Caltha* (cushion form), *Carpha, Colobanthus, Gunnera, Marsippospermum, Pernettya, Pratia, Rostkovia* and *Tetrocium* mix with cosmopolitan *Alopecurus, Carex, Juncus* and *Primula*. (Skottsberg 1960, Troll 1978).

b. Bryophytes

The early collections from Tierra del Fuego consisted mainly of vascular plant but some bryophytes were also included and thus the check-list by Moore (1983a) naming the collectors of vasculars is relevant for bryophytes also. Conspicuous and recognizable species of Polytrichaceae such as *Polytrichadelphus magellanicus* and *Dendroligotrichum dendroides* were collected e.g. by Philip Commerson in 1767 during the first scientific voyage by the Bougainville (Cardot 1908). Alexander Menzies visited Tierra del Fuego and Staaten Island two decades later on the Vancouver voyage also collecting bryophytes (Bescherelle 1889). The first hepatic sample is of one *Jungermannia magellanica* by Commerson (Hässel de Menéndez & Solari 1975, Geissler & Bischler 1987).

Since the early 19th century the number of moss records from Tierra del fuego was gradually increased by several authors (e.g. Hooker & Wilson 1844, Mitten 1860, Müller 1885). The bryological results on mosses of the firts Swedish expedition to the Magellanic region in 1896-97 were presented by Dusén (1903b, c, 1905a, b, 1906a, b). Hepatics were treated by Stephani (1900, 1901, 1911) who also published the results on hepatics collected by Skottsberg during the second expedition in 1901-03 (Stephani 1905). Other important contributions on hepatics were given by Hooker & Taylor (1844). Massalongo (1885), Bescherelle & Massalongo (1889), Evans (1898) and by Stephani mentioned above. Stephani (1911) also published the hepatic collections of the third Swedish expedition in 1907-09. The mosses collected by Skottsberg in 1901-03, 1907-09 and 1917 formed the base of the respective works by Cardot (1908), who summarized all records from more than a century of exploration, Cardot & Brotherus (1923) and Brotherus (1924).

Studies on the bryophyte material collected by the Finnish expedition to Tierra del Fuego in 1928-29 were published by Roivainen (1954a, b, 1955), Roivainen & Bartram (1937) and Bartram (1946), and by Engel (1976, 1978). Roivainen returned to Tierra del Fuego in 1969-70 for another collection trip (Roivainen 1972). The studies by Thériot (e.g. 1915, 1921), Herzog (e.g. 1922, 1938), Reimers (1926) and Malta (1927) were based on collections from further north but included many species reaching Tierra del Fuego

Gradually briological studies were also undertaken by Argentine botanists. Kühnemann published Argentine check-lists on both mosses (Kühnemann 1938) and hepatics (Kühnemann 1949). Presently studies in Tierra del Fuego are mainly conducted by Argentine bryologists such as Matteri (e.g. 1968, 1973, 1975, 1984) on mosses and Hässel de Menéndez (e.g. 1967, 1974, 1983, Hässel de Menéndez & Solari 1975) on hepatics. Studies undertaken by British bryologists (e.g. Bell 1973, Clarke 1973, Newton 1974, S. Greene 1975, Lightowlers 1986 and Finnish (Hyvönen 1987, 1991), German (e.g. Schultze-Motel 1970, Frahm 1975, 1981, Menzel 1988), Polish (Ochyra 1987) and Japanese briologists (Inoue 1972, Seki 1974, Ochi 1982, Deguchi 1984) in the adjacent areas should be mentioned for the numerous shared taxa in the circumantarctic area. The check-list by D. Greene (1986) forms a good basis for all floristic studies in the area. There are also remarkable contributions by North American bryologists dealing with southern South America (Schuster e.g. 1967, 1969, Engel e.g. 1976, 1978).

Estimates of the number of bryophyte species in Tierra del Fuego vary as the taxonomy of several groups is still obscure. The flora of Cardot (1908) remains the most comprehensive work on mosses (Hässel de Menéndez et al. 1984). Lately many new taxa have been described and some groups monographed. According to Kühnemann (1979) there are ca. 400 mosses and 300 hepatics in Tierra del Fuego. The actual number may be 10-20% lower as put forward by Hässel de Menéndez et al (1984) for Patagonian mosses.

The peculiar distribution of many of the southern vascular plants (e.g. *Nothofagus*) representing the assumed old Gondwana-element is shared by many bryophyte groups as well, e.g. genera *Leptostomum* and *Polytrichadelphus* in mosses and *Temnoma* and *Herzogobryum* (Schuster 1983) in hepatics. The primitive, fairly generalized taxa are relatively abundant in the hepatic flora of the area. They are interpreted to be relicts of ancient Permian *Glossopteris* flora (Schuster 1983) adapted to cool conditions.

More puzzling is the origin of bipolar distribution patterns as exemplified, for example, by bryophytes such as *Sphagnum magellanicum, Ptilidium ciliare* and several others. The topic has been discussed extensively and most often distribution is explainded by long-range dispersal. However, these theories have not recieved universal acceptance (Humphries & Parenti 1986). It is postulated that the successful long-range dispersal of propagules is possible by air-currents at fairly high altitudes. This has been proved to be true for several taxa in the elegant experimental studies by van Zanten (1976, 1978) and van Zanten & Gradstein (1987). Studies by Smith (1987) have also shown that the propagules of numerous taxa remain viable on ground even in very harsh enviroments and include also spores from remote localities. However, the actual success of establishing at a new site is dependant also of many other factors such as competition and availability of suitable habitats as well as the general ecological requirements of each particular taxon. The relatively low number of species with "circumantarctic" distribution (Schuster 1983), despite the abundance of propagules and favorable strong air currents, illustrates that no general or simple solutions are available to explain the present distribution patterns. Cladistic studies of several bryophyte groups such as the revision of genus *Scouleria* by Churchill (1985) will facilitate the use of the methods of vicariance biogeography. These studies will help in their own way to form the correct interpretation of present ranges of the taxa. However, in many bryophyte groups the lack of basic modern revisions still prevents the critical biogeographical analysis. The crucial importance of reliable taxonomy is further augmented by the fact that bryophtes are important or even dominant members of many vegetation types. Rapid progress is, however, to some extent hindered by the scarcity of local bryologists (Matteri 1985).

c. Lichens

Since the 19th century lichens have been observed, collected and studied by numerous lichen taxonomists and other naturalists. Nylander (1888) reported 141 lichen species from Tierra del Fuego and Patagonia. Other notable contributions are those by Crombie (1877), Vainio (1887, 1894), Hariot (1887), Müller Argoviensis (1889), Jatta (1890), Zahlbruckner (1917), Du Rietz (1926b) and Cengia-Sambo (1926a, b, 1928). Räsänen (1932) published the material collected by H. Roivainen in 1928-29. The considerable literature on the records published prior to 1950 is summarized by Grassi (1952).

In recent decades few extensive papers have been published on the lichen flora of southern South America. Nevertheless, valuable information can be found in a number of taxonomic studies (Santesson 1942, 1944, Burkholder et al. 1965, Dodge 1965, 1966, Krog 1976, Redón & Quilhot 1977, Ahti & Kashiwadani 1984, Redón 1985, Walker 1985, Galloway 1986 and Stenroos 1987). Follmann (1961) presents a list of the most important collections of Chilean lichens. The chemistry of Fuegian lichens has been studied by e.g. Sahina (1965) and Hawksworth & Moore (1969). An extensive bibliography is given by Osorio (1987) who lists the publications on Argentine lichens issued in 1950 to 1985.

Lichens represent an important and conspicuous element of the flora in many parts of Tierra del Fuego. Notwithstanding the interest on the lichens of Tierra del Fuego during the present and past century, the composition of the lichen flora (crustose lichens in particular) is imperfectly known. Grassi (1950) listed ca. 310 lichen species reported from Tierra del Fuégo. Identifications reported in the early works need re-examination in the light of recent progress in the lichen taxonomy and chemistry.

In the steppe area the macrolichen flora is very poor. The dominant species include the terricolous lichens *Peltigera rufescens* s. lat., *Psoroma hypnorum f. cinnamomeum* and some members of the genus *Cladonia* (e.g. *C. chlorophaea* and *C. pocillum*). The lichens are especially luxuriant in mixed as well as deciduous forests, where epiphytes are abundant. Numerous species of *Pseudocyphellaria* cover the tree trunks and in places also the forest floor. Other dominants include the species of the genera *Menegazzia, Sticta, Usnea, Protousnea, Leptogium* (mainly *L. menziesii*), *Peltigera* (e.g. *P. rufescens* and *P. polydactylon* s. lat.) and *Nephroma* (mainly *N. antarcticum* var. *antarcticum*) as well as some members of the family Pannariaceae. The rainforests have their own, peculiar lichen flora. Species of *Pseudocyphellaria* and *Nephroma* still dominate, but the most conspicuous lichens are perhaps the large tufts of *Sphaerophorus tener* and *S. melanocarpus*, which grow on branches of *Nothofagus betuloides*. The members of the family Cladoniaceae are most common in bogs, which are often rich in *Cladia aggregata, Cladina rangiferina, C. mitis, C. arbuscula, C. pycnoclada, Cladonia bellidiflora* and *C. squamosa*. Furthermore, the species of *Usnea* subg. *Neuropogon,* which cover the rocks of the highest mountain peaks and are visible from far due to their bluish black colour, deserve to be mentioned.

The degree of endemism in lichens in the far south is low when compared to that of phanerogams (Jorgensen 1983). Bipolar species are numerous in Tierra del Fuego, at least in some groups: e.g. 18 species out of 37 in the family Cladoniaceae are bipolar in their distribution (Stenroos 1987). Several species of the genus *Peltigera* also show a similar distribution pattern (O. Vitikainen, pers. comm.). The affinities of the lichen flora in SE Australia, Tasmania, New Zealand and southern South America have been discussed by several authors. The socalled austral element is the most prominent in the *Nothofagus* forests, where many taxa (e.g. the memebers of the genera *Pseudocyphellaria* and *Menegazzia*) are related to those in the ecologically similar Australasian forests of *Nothofagus* (Jorgensen 1983). Galloway (1987) divides the austral element into palaeoaustral and neoaustral groupings, i.e. those taxa which represent the former Gondwanan vegetation, and those which have dispersed after the fragmentation of Gondwana, respectively. Plate tectonics as a background of the present distribution of lichens has been discussed by Galloway (1988), who also gives a valuable bibliography.

2. *Vegetation*

The general basis of the presentations on the vegetation of Tierra del Fuego has traditionally been the readily visible system of the extensive physiognomic units running parallel to the Andes from barren rocks and wet heaths and rainforests in the west to steppes in the northeast (Fig. 21)

The physiognomic Fuegian system has already been reviewed by the Bougainville (1771), King (1832), Webster (1834), Dumont D'Urville (1841-46), Hooker (1847) etc. and often referred as the "Fuegian vegetation zones". Major phytogeographic works based on the early explorers' journals include Grisebach (1872), Lorentz (1876), Engler (1879), Drude (1890), Warming (1895) and Schimper (1898). These comprehensive manuals and the erarly monographs on the vegetation of southern South America by Dusén (1903a), Reiche (1907) and Skottsberg (1909, 1910, 1916) probably resulted in some decreasse of interest in vegetation studies in that area during the subsequent decades. New original material was scarce till 1960's (The Royal Society Expedition, see Godley 1963; Instituto de la Patagonia, see Pisano 1970 etc.) from the southern latitudes 42° to 56° S. The recycling of old material and the great amplitude of climatic conditions and dominant growth forms over short east-west distances caused a lasting confusion of terminology upon the vegetation of Tierra del Fuego and Patagonia (e.g. Pérez-Moreau 1944, Pérez-Moreau & Sgrosso 1949, Deacon 1960).

Reinward (1849), Cunningham (1871a), Savatier (1880), C. Martín (1882), Nordenskjöld (1897a), Dusén (1896, 1898,1903a, d), Reiche (1907) and Skottsberg (1909,1910, 1916) give the firts detailed descriptions on vegetation in southern outh America. Thir material was used in subsequent phytogeographic manuals, e.g. Cajander (1916), Warming & Graebner (1918), Rübel (1930) and Schimper & von Faber (1936). The material of Reiche (1907) and Skottsberg (1916) was used by Oberdorfer (1960) for the classification of the vegetation of southern Patagonia.

Accurate and modern regional studies on the western Magellanic vegetation have been conducted in by Alfonso (1942), Cozzo (1949), Godley (1960a), Holdgate (1961a), Correa Luna (1964), Young (1972), Crow (1975), Kühnemann (1976), McQueen (1976,1977), Dudley & Crow (1983), Bianciotto (1985), Brion et al. (1988), Matteri & Schiavone (1988) and Collantes et al. (1989c). Instituto de la Patagonia in Punta Arenas deserves a special mention having hosted the work by Pisano (1970, 1971a, b, 1972a, b, 1973, 1977a, 1980, 1981, 1982, 1983a, b), Dollenz (1980, 1981, 1982a, b, c, including direct relevée data), Pisano & Schlatter (1981a, b) and Pisano & Venegas (1984).

Vegetation studies on the Magellanic steppes include Davies (1940), Pisano (1971a, 1974), Pisano & Dimitri

(1973), Dollenz (1977, 1978), Duga (1980), Collantes et al. (1985), Cagnoni et al. (1989), Collantes et al. (1989 a, b). Peatland vegetation has been treated by Roivainen (1954a), Schwaar (1976, 1979, 1981), Moore (1979), Pisano (1983a), and Roig (1984). Comprehensive treatments on the vegetation of the Magellanic area are presented by Pisano (1977a, 1981) and Moore (1983a), Knapp (1966) lists the higher vegetation units of Fuegia.

A major effort was in the study of he vegetation of southern Patagonia (Región de Magallanes and Provincia de Santa Cruz) made with the Transecta botánica de la Patagonia austral in the late 1970's (Soriano et al. 1983, Roig et al. 1983, Roig 19 4, Boelcke et al. 1985, Seibert 1987). Earlier studies include work such as that of Kölliker 1917, Hosseus 1918, Hauman 1920, 1926, Davies 1940, Kalela 1941, Kalela 1941a, b, c, d, Pérez-Moreau 1946, 1959, Pisano & Dimitri 1973, Dollenz 1982b, Veblen et al. 1979.

More general descriptions on the Fuegian-southern Patagonian vegetation and phytogeography include these by Hicken (1915), Neger (1917), Spegazzini (1923), Roivainen (1930), Skottsberg (1932), Auer (1933, 1963), Castellanos (1938), Alfonso (1940), Fiorda (1940), Pérez-Moreau (1945), Goodspeed (1945), Dimitri (1964), Pyykkö (1968), Peña & Barrio (1972), Solbrig (1984) and Tuhkanen & Niemelä (1989).

Concise presentations on the vegetation of southern South America are found on a general level: e.g. Walter (1968), Hueck & Siebert (1972) and UNESCO (1981). The Argentine has been presented by Castellanos & Pérez-Moreau (1944), Kalela (1945, 1946), Kühn (1947), Hauman (1947), Papadakis (1958), Cabrera (1958, 1978) and Küchler (1981). Outlinings on Chilean vegetation include Fuenzalida (1950), Pisano (1950, 1956), Schmithüsen (1956), Mann (1960), Oberdorfer (1960), Hueck (1966), Donoso (1981), Quintanilla (1983), Veblen et al. (1983).

There are a few studies dealing with vegetation from the natural resources and land use point of views. The Fuego-Patagonian-Falklandic steppe area has been examined in this way by Spegazzini (1911), Davies (1939, 1940), Fiorda (1940), Roseveare (1948), Ragonese (1967), Serra (1970) and Duga (1980). The respective forested area is more thoroughly covered. General presentations include Kozdon (1955, 1958), Hueck (1966), McQueen (1976, 1977) and Veblen et al. (1983). The Argentine forests have been reviewed by Spegazzini (1910), Rothkugel (1916), Alfonso (1940, 1942), Kalela (1941a, b, c), Parodi (1945), Tortorelli (1945, 1956), Dimitri (1964, 1972) and Servicio Nacional Forestal (1972). Chilean works include Reichenstein (1951), Clarke (1964), Instituto Forestal de Chile (1966) and Donoso (1981). Bonarellu (1917), Guiñazu (1934) and Martín (1949) worked on peatland resources. Land use potentials have been discussed by Auer (1951a), Parodi (1964) and Seibert (1987). Auer (1949, 1951b) commented on the retreat of forests.

The ecology of the southern vegetation has been covered by Alfonso (1940, 1942), Holdgate (1961a, b), Kubitzki (1964), Huntley (1972), Young (1972), Weinberger (1973), Weinberger et al. (19737, Moore & Doggett (1976), McQueen (1976, 1977), Walton (1979), Seibert (1980, 1987) and Roig et al. (1983). The dynamics of the forest-steppe ecotone have been studied in Tierra del Fuego by Auer (e.g. 1933a, 1935, 1939, 1946, 1951b, 1958a) and in Patagonia by Kalela (1941a, d) and Eriksen (1972). Some forestry studies from Patagonia include material on vegetation dynamics in *Nothofagus* communities (e.g. Kalela 1941a, b, d, Kozdon 1958, Veblen et al. 1979, Donoso 1981). Klötzli (1983) compared the ecology of *Fagus* and *Nothofagus*. Peatland ecology in Tierra del Fuego has been treated by Roivainen (1945a) and Roig et al. (1983).

Vegetation transect profiles in various scales have been presented by Martín (1949), Schmithüsen (1956), Holdgate (1961a), Auer (1963), McQueen (1976), Alhonen & Auer (1979), Donoso (1981), Dollenz (1977, 1981, 1982b, c). Czajka (1968) compiled a longitudinal vegetation profile along the Cordilleran chain from Alaska to Tierra del Fuego while Garleff's (1977) provided transects across the Fuego-Patagonian Andes showing the general distribution of the dominant tree species.

Dusén (1903a, 1906), Skottsber (1906, 1909) and Bonarelli (1917) were the first to publish simple vegetation maps from Tierra del Fuego and southern Patagonia. Skottsberg (1910) presented a detailed and accurate map of the large vegetation formations of western Fuego-Patagonia while Skottsberg (1916) included local vegetation maps. Skottsberg (1932) and Correa Luna (1964) give the drought limits of *Nothofagus*. Maps based mainly on physiognomic vegetation units have since been outlined by Godley (1960a, reprinted by McQueen 1976), de Laubenfels (1970), Hueck & Seibert (1972), Young (1972), Goodall (1979), UNESCO (1981), Donoso (1981), Veblen et al. (1983), Moore (1983a), Markgraf (1983), Bondel (1988), Tuhkanen & Niemelä (1989). Frederiksen (1988) provided a more detailed map based mainly on satellite images. Outlings limited to Chile include Pisano (1950), Schmithüsen (1956), Mann (1960), Donoso (1981) and Quintanilla (19837. Those covering mainly Argentine territories are by Davies (1940), Castellanos & Pérez-Moreau (1941-1944), Kalela (1946), reprinted by Pyykkö (1968), Papadakis (1958, reprinted by Agro -Palermo 1983), Duga (1980) and Soriano et al. (1983).

Pisano (1977a, 1981) presented the areal distribution of the dominant plant communities in Chilean Tierra del Fuego. Local maps on dominant communities have been published by Pisano (1973a, 1983b), Pisano & Dimitri (1973), Dollenz (1977, 1978), Pisano & Venegas (1984) and Collantes et al. (1985). Detailed maps of the major plant communities from the "Transecta botánica de la Patagonia austral" transect can be found in Roig et al. (1983), Boelcke et al. (1985) and Seibert (1987). Bonarelli (1917), Roivainen (1954a), Auer (1963) and Alhonen & Auer (1979) present maps on peatland vegetation in Tierra del Fuego. An index of the vegetation maps on Argentina is given by Cano & Gómez (1968). According to Küchler (1981) the Magellanic region is one of the best mapped regions in the Argentine from a vegetation point of view.

Early outlines of the Argentine floristic-phytogeographical districts were mapped by Lorentz (1876), Holmberg (1898), Rovereto (1914), Hauman (1920b, 1931), Kühn (1930, 1947), Instituto Geográfico Militar (1934), Parodi (1934, 1945, 1964), Frenguelli (1941), Parodi et al. (1947) and Cabrera (1953). The latter includes a review of most of the early outlinings. Cabrera (1971) follows Cabrera (1953); Hauman et al. (1947), Parodi (1964), Ragonese (1967) and Servicio Nacional Forestal (1972) follow Parodi (1945); Soriano (1956) and Cabrera (1978) follow the vegetation maps by Davies (1940) and Castellanos & Pérez-Moreau (1941, 1944).

Circumantarctic vegetation has been treated at a general level by Schenk (1950) Skottsberg (1905b), Oliver (1925), Raunkiaer (1936), Troll (1948, 1960), Pérez-Moreau & Sgrosso (1949), Du Rietz (1960), Godley (1960a), Wace

(1960, 1965), Greene (1964), Schmithüsen (1964), Brundin (1966), Longton (1967), McQueen (1976), de Moral (1978), Bliss (1978), Moore (1979), Veblen et al. (1983) and Hämet-Ahti (1986). Bipolar relations are discussed by Troll (1948), Oberdorfer (1960), Schwaar (1981) and Klötzli (1983) while Troll (1948, 1960), Bader (1960) and several autohors in Troll & Lauer (1978) focus towards low latitude mountains.

Hieronymus (1885), Rühle (1928) and Schmithüsen (1956) followed the German climatic vegetation concept of Grisebach (1872) and Schimper (1898) looking for correlations between climates and vegetation formations or major physiognomic vegetation units. Troll (1948, 1960) and Gams (1957) speak of microthermal vegetation. George (1946), Bagnouls & Gaussen (1957) and di Castri (1968) outline general climatic-based divisions. Pisano (1977, 1981) presents Fuegian vegetation using climatic regions based on the modified Köppen system for the higher classes.

Zonal outlinings on the Circumantarctic were put forward by Schouw (1822) and Delpino (1897) who spoke of cold temperate vegetation and De Candolle (1855) who proposed the use of the term austral . Skottsberg (1905b, 1960) launched the wide use of the Subantarctic zone with uniform vegetation physiognomy in the area of cool west winds. The subantarctic zone was delimited or discussed by for instance Brockmann-Jerosch (1928), Nordenskjöld (1928), Rudmose Brown (1928), Lindsay (1940), Deacon (1960), Wace (1960, 1965), Greene (1964), Longton (1967), Gressitt (1970), Holdgate (1970), Bliss (1978) and Aleksandrova (1980). Subantarctic was often applied rather freely covering as much as latitudes between 35-60° S or overlapping with Antarctic and antitemperate wherefore Augener (1932) and Ekman (1935) suggested an antiboreal zone. The Finnish bioclimatic system of zonation using the boreal equivalent of antiboreal was presented by Tuhkanen (1984, 1986, 1987, and in press and Hämet-Ahti (1986). Raunkiaer (1936) and Pérez-Moreau & Sgrosso (1949) presented the southern chamaephyte zone. The list of cultivated plants in Tierra del Fuego (Milano & Marzocca (1954) and experiments by South American *Nothofagus* in Britain (Nimmo 1979) or on the Faeroes (Hansen & Odum 1982, Tuhkanen 1987, Odum et al. (1989), for instance, give also phytogeographical information from the zonation point of view.

The steep climatic gradient across Tierra del Fuego from the west and southwest to the northeast, i.e. from extremely oceanic and humid to semi-arid and markedly less oceanic conditions, determine, in combination with soils, the broad pattern of the distribution of the principal physiognomic units of vegetation. As a result, four major vegetation formations are usually distinguished: Fuego-Patagonian steppe, Deiduous forest, Evergreen (rain) forest and Magellanic moorland. In the transition between steppe and closed forest, deciduous and, to a limited extend, even evergreen woodlands occur, and between deciduous and evergreen forests, mixed forests. In response to changes in thermal, humidity and exposure conditions varying with altitude in the mountains, changes in vegetation occur, one of the most marked of these being the transition from forest to treeless "alpine" vegetation. The highest Fuegian sierras are covered by permanent snow and glaciers. Within the range of each formation local environmental conditions vary substantially, and numerous different communities can be recognized. Only the main features can be described below.

The mire vegetation will also be discussed because of its predominance in many parts of Tierra del Fuego, although certain other more local communities such as aquatic vegetation, will not be dealt with.

a. Steppe

The southernmost extension of the East Patagonian treeless plateau covers some 40% of northern Isla Grande where rainfall is less than about 350-400 mm per year. The altitudinal range reaches 600 m at athe Altos del Boquerón and 300 m at Sierra Carmen Sylva, but the dominant landscape is an undulating plain below 100 m altitude with an insignificant gradient. Few brooks or rivers (Río Grande system, Río Chico) have carved deep channels in the open plateau. The steppe soils, in general developed from glacial till deposits with a loess sheet, are slightly or moderately leached, not very acid, and tend to be relatively fertile. There are also in abundance very gravelly and sandy glacial meltwater deposits with meagre nutrient properties.

The Fuegian steppe can be distinguished from the Patagonian counterpart by higher humidity (Eriksen 1983). The ecological differences gave rise to the distinction between southern (Magellanic-Falklandic) and northern (Patagonian) floristic regions within the treeless pampas (Ball 1887, 1891, Skottsber 1904, 1905b, 1910, 1932, Donat 1932, Beetle 1943). They generally agree that the boundary follows about the course of Río Coyle lying at 52° S in the east and turning northwards in the west. There is also a difference in the dominant vegetation, i.e. tall scrub, tussock grassland or grass heath in the south (Fig. 22) vs. dwarf scrub-cushion plant-low grass mosaic in south-central Patagonia. Thus northern Fuegia and southern Patagonia can be treated as steppe while Patagonia further north is semi-desert with a relative abundance of xerophytic and annual plants as discontinous vegetation. The subhumid (Subandean) tussock grassland type continues along the westside of

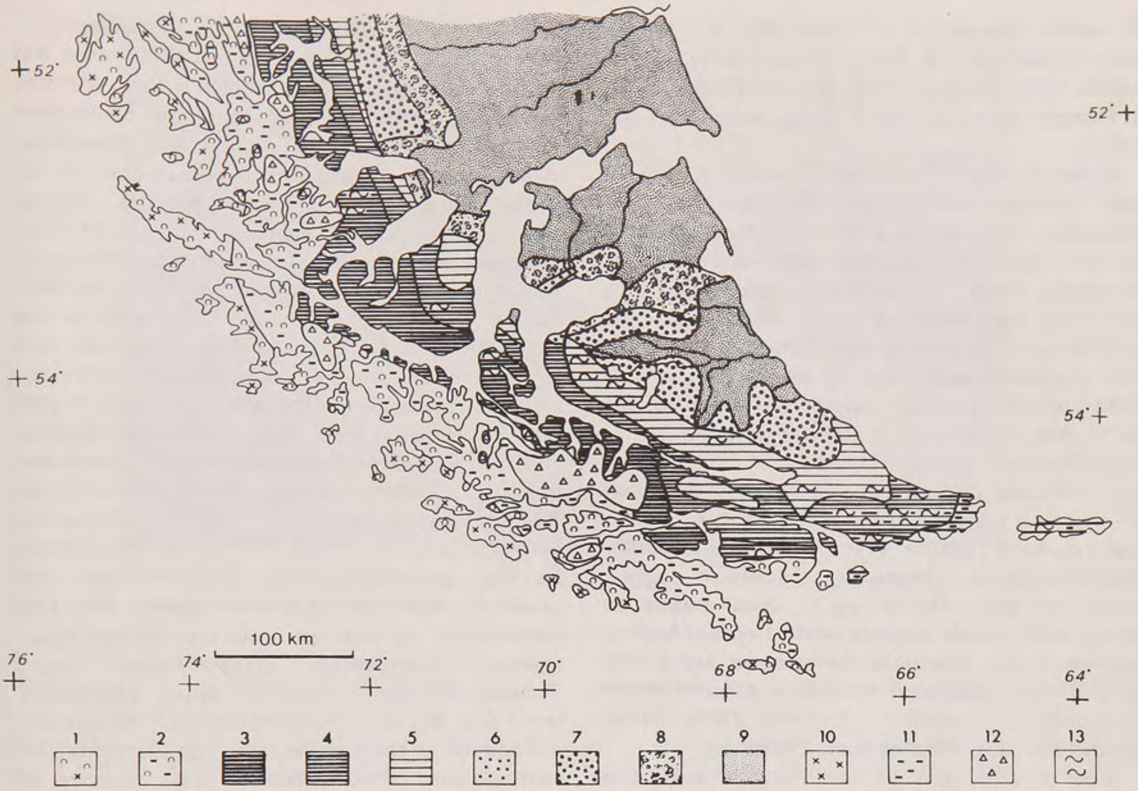

Fig. 21. The main vegetation formations in Tierra del Fuego. Based on data from existing literature, especially on the maps of Godley (1960), Young (1971), Pisano (1977), Moore (1983a) and Frederiksen (1988: plate 2), but modified on basis of observations made in the present project.

VEGETATION FORMATIONS IN TIERRA DEL FUEGO

1. Predominantly exposed igneous rocks without vegetation of the outermost Pacific islands. Scrub forest (*Nothofagus betuloides-Drimys winteri*) mixed with dense shrubbery in sheltered locations.
2. Blanket bogs (*Astelia pumila-Schoenus antarcticus)* with scattered *Pilgerodendron uviferum* stands of the outer Pacific archipelago. Forests of type 3 in shelter and scrub of type 1 on exposed hillsides.
3. Dense dark evergreen forests (*Nothofagus betuloides-Drimys winteri*) of the inner Pacific archipelago with a continuous cover of *Hymenophyllum* spp. and Hepaticae. Blanket bogs of type 2 frequent on level land. Sic: Sparser hatchng when mixed with 2.
4. Mixed evergreen (*Nothofagus betuloides-Drimys winteri*) and deciduous (*Nothofagus pumilio-Nothofagus antarctica*) forests, often multistoreyed including tall shrubbery. Field layer predominantly herbaceous, ground layer predominantly of mosses.
5. Deciduous forest of *Nothofagus pumilio* with poor undergrowth (at least partly owing to grazing by guanacos). The evergreen component lacking.
6. Evergreen woodland of *Drimys winterii, Maytenus magellanica* and *Embothrium coccineum*. Originally with a scarce herbaceous undergrowth, but sometimes invaded by the shrubbery of type 8.
7. Woodland or forest island ("park forest") of the deciduous beeches (*Nothofagus antarctica-N. pumilio*) with undergrowth dominated by grasses. Lowlands often form climatic steppes or poorly drained grass fens.
8. *Chiliotricum diffusum* dominated shrub steppe rich in dwarf shrubs and booth forest and steppe herbs. Grass-sedge fens occur in the lowlands.
9. Magellanic bunch grass steppe (*Festuca gracillima*) with many tiny shrub herbs and semiwoody dwarf shrubs. Valley lowlands often dominated by grass fens.
10. Exposed rocks, abundant.
11. Cushion heath (*Astelia*).
12. Glacier.
13. Raised or sloping bogs (*Sphagnum magellanicum*) abundant.

the whole Patagonia to about 35° S. (Davis 1940, Castellanos & Pérez-Moreau 1941, 1944, Kalela 1946, Soriano 1956, Pyykkö 1968, Pisano & Dimitri 1973, Cabrera 1978, Soriano et al. 1983).

In northeastern Tierra del Fuego low steppes with modest grasses like *Deschampsia* spp. *Hordeum comosum, Trisetum spicatum* and *Agrostis* spp. and various semiwoody dicotyledoneous herbs with hardened basal parts and withering tops (*Suaeda* spp., *Valeriana* spp., *Senecio* spp., *Artemisia magellanica).* There are also important portions of ground geophytes *(Phaiophleps biflora, Sisyrinchium patagonicum),* rosette (*Senecio* spp., *Boopis* spp., *Silene magellanica, Armeria maritima, Geranium* spp., *Acaena pinnatifida, Calceolaria uniflora)* or creeping (*Arjona* spp., *Adesmia* spp.) herbs and cushion plants (*Frankenia chubutensis, Nardophyllum bryoides, Azorella* spp., *Nassauvia* spp., *Draba* spp.). Near coasts on sandy soils shrub steppes with *Lepidophyllum cupressiforme, Adesmia boronioides* are found and on tide inluenced mud flats *Eriachaenium magellanicum* scrub. (Dollenz 1977, 1978, Pisano 1977a, Collantes et al. 1989a, b).

The greater part of the Fuegian steppe is covered with monotonous vegetation dominated by *Festuca gracillina* tussock grassland and *Chiliotrichum diffusum* scrub or their mosaic. The coastal strip in the central strait area has additional Asteraceous (*Baccharis* spp., *Perezia recurvata, Senecio patagonicus*) or Ericaceous *(Pernettya mucronata)* shrubs and *Blecchum penna-marina* forming impenetrable scrub on higher grounds and windward hillsides. In the scrub *Festuca* tussocks are absent and instead rhizomatous grasses like *Bromus unioloides, Phleum alpinum* and *Agropyron* spp. are found. As the rainfall in the northeastern coastland falls to less than 300 mm *Chiliotrichum* scrub breaks into grass-shrub mosaic and retreats to sheltered sites. In windy lowlands shrubs fade completely to give way to a uniform *Festuca* grassland with *Agropyron* spp. and dicotyledoneous herbs (*Acaena magellanica, Taraxacum* spp., *Calceolaria biflora, Ranunculus peduncularis, Rumex acetosella*) between tussocks. Towards interior Isla Grande *Festuca gracillima* and *Chiliotrichum* are gradually replaced by smaller grasses like *Poa alopecurus, Agrostis* spp. and *Deschampsi* spp., rossette composites (*Hypochoeris* spp., *Taraxacum* spp., *Erigeron* spp., *Hieracium* spp.) and *Berberis buxifolia* scrub. Mosses are infrequent in the steppe area, but *Acrocladium auriculatum, Brachythecium* spp., species of Bryaceae, *Pseudoleskea chilensis, Tortula* spp., and some other species of Pottiaceae are

Fig. 22. The semi-arid northern parts of the main island of Tierra del Fuego are characterized by the tussock grass steppe with *Festuca gracillima* as dominant. Photo shows a part of the western extension of the steppe, northward of the Rio Grande river. Photo: Sakari Tuhkanen (1985).

Fig. 23. In the transition zone between steppe and forest (= kampfzone, whose dynamics have been discussed by Auer (1933) and others), woodland island on elevated areas and vega grasslands in depressions characterize the landscape. The tree is *Nothofagus antarctia*. Photo: Sakari Tuhkanen (1987).

characteristic in small quantities (Dusén 1903a, Reiche 1907, Davies 1940, Pisano 1971a, 1977a, Moore 1983a). Knapp (1966) placed the scrub into Chiliotricho-Berberidetalia order and the grassland into Acaeno-Festucetea gracillimae class. Pisano (1977a) recognized Festucetum gracillimae (grassland), Festuco-Chiliotrichietum diffusii (mosaic) and Chiliotrichietum diffusii (scrub) associations.

Cushion plant heaths formed by *Bolax gummifera* develop under exposure to strong oceanic winds of moderate humidity. These heaths consisting of hard hummocks are found in the area of relatively humid steppes (the southern Altos de Boquerón and Sierra Carmen Sylva). The associates on the hummocks include *Azorella* spp., *Festuca gracillima* and creeping *Acaena magellanica* and *Pernettya pumila*. Sometimes there is transgression towards *Polytrichum* bogs.

In windy lowlands of interior Isla Grande on coarse, nutrient-poor substrate tussock grasses and broad-leaved herbs fade for heath vegetation formed by creeping dwarf shrubs (*Empetrum rubrum, Baccharis* spp., low grasses (*Agrostis flavidula, Deschampsia flexuosa*) and cushion or other hummock-forming plants (*Azorella* spp., *Bolax gummifera, Polytrichum strictum*).

In central Isla Grande the limit between forest patches and lowland grassland (Fig. 23), affected to a great extent by bad drainage and cold night air, is sharp. Waterlogging of the valley floors in the early summer owing to flat relief prevents the trees and shrubs from spreading onto the humic so-called vega meadows (Dusén 1903a, Davies 1940, Moore 1983a). Thus in several interior low altitude valleys the grasslands reach the foot of the Marginal Cordillera. The vega meadows are commonly composed of various grasses (*Hordeum comosum, Phleum alpinum, Alopecurus magellanicus, Trisetum spicatum*), sedges (*Carex macloviana, C. decidua, C. gayana*), rushes (*Luzula alopecurus*) and few herbs (*Geum magellanicum, Ranunculus peduncularis)*. They also support a fairly rich bryophyte flora, e.g. *Plagiomnium rugicum, Sanionia uncinata* and *Drepanocladus exannulatus*.

b. Evergreen woodland

In limited areas in both sides of the mouth of Bahía Inútil evergreen woodlands are found these develop only in mild coastal climates where they occur between forest and deciduous woodland communities. In the eastern Peninsula Brunswick area, near Punta Arenas, the evergreen woodland is extinct, but at the south side of the mouth of Bahía Inútil natural roundtopped *Drimys-Maytenus magellanica* stands with occasional *Nothofagus* still prevail on the coastal hills between tall deciduos-evergreen forest and grass steppe. Owing to a thick layer of wet leaf litter the undergrowth is sparse despite abundant light. *Drimys* seedlings are conspicuous with scattered *Adenocaulon chilense, Blechnum penna-marina, Codonorchis lessonii, Gavilea lutea* and *Osmorhiza* spp. *Embothrium coccineum* is absent from mature stands but it is a member of marginal communities (Pisano 1973a).

On the coastal slopes of the Altos de Boquerón, a fairly large area of evergreen woodland has existed (Pidano 1977a). Even a stand of *Nothofagus* was photographed by Auer (1933a: Fig. 81), but the genus is nowadays extinct in the area. Unfortunately, under a century of human disturbance a greater part of the woodland has been destroyed. The small central part probably possessed a *Drimys-Maytenus* woodland similar to the opposite side of the bay. Around this existed a sparser *Maytenus-Embothrium* community (Fig. 24) and still further an *Embothrium* community having a form reminiscent of tree savanna. Their original vegetation can only be speculated upon, as frequent fires have led to an aggressive advance of *Chiliotrichum difusum*. In the *Maytenus* dominated community *Pernettya mucronata, Polystichum multidifum* and *Blechnum penna-marina* may have been characteristic and probably also *Ribes magellanicum* and *Berberis buxifolia*. Evidently the weak ecotonal *Embothrium* community is least changed having tall undergrowth of *Chiliotrichum, Ribes* and *Berberis*. The evergreen woodland has a sparse but diverse bryophyte flora *Acrocladium auriclatum, Bartramia halleriana, Brachythecium* spp., *Bryum* spp., *Lepyrodon lagurus, Tortula* spp. and *Leptoscyphus expansus* being most conspicious.

c. Deciduous woodland

A zone of *Nothofagus antarctica* woodland occurs in central Fuegia forming an ecotone between continuous forests and steppes. Low

Fig. 24. Relict stand of once extensive *Maytenus magellanica, Embothrium coccineum* woodland at 250-300 m altitude on southern slopes of Altos de Boquerón. *Drimys winteri* occur lower down. Regresive development of these forests is mostly due to human impacts. In this region some *Nothofagus* trees, now totaly disapeared, were seen by Auer as late as 1929 (Auer, 1933: 271). Photo: Ilpo Kuokka (1986).

open tree stands predominate on ridges in the broad Río Grande basin and between rivers east of the basin (Skottsberg 1910, Godley 1960a, Frederiksen 1988). Hills and divides are as a rule wooded while lower parts of the terrain are steppe (Fig. 23). On higher hills taller *Nothofagus pumilio* is often found in the centres of the wooded islands. Annual rainfall within this zone is 350-500 mm.

Nothofagus antarctica is not an independent forest forming species, but at the southern Fuego-Patagonian steppe margin it has no competitors. Its trunks are generally more or less bent and somewhat spirally creeping or ascending. It propagates asexually from basal shoots and rooting branches that produce radial clusters of trunks. Old trees seldom die as the clone continuously replaces older parts by new regrowth. Marginal *N. antarctica* stands are frequently open with ragged canopies having about 50% coverage when abundant light contributes to a conspicuous undergrowth of *Chiliotrichum diffusum* and *Berberis buxifolia* shrubs (Fig. 25). At the grassland edge the community is dense and more dynamic.

The coastal woodlands on the east-central Atlantic coast of Isla Grande are more mesic and closed than most interior stands. There are almost no shrubs but the herbaceous growth is rich (*Cystopteris fragilis, Galium* spp., *Osmorhiza* spp., *Acaena* spp., *Blechnum penna-marina, Viola maculata*). *Bromus unioloides* is a conspicuous grass. The dry interior variants on higher ground or on gravelly substrates differ form the coastal woodlands by the absence of broad-leaved herbs and the presence of graminoids (*Festuca magellanica, Trisetum spicatum, Deschampsia flexuosa, Luzula alopecurus*), geophytes (*Phaiophleps biflora, Sisyrinchium magellanicum*) and creeping herbs (*Cerastium arvense, Cotula scariosa*). The lowlands in the western Río Grande basin recieve more moisture (e.g. snow) and the forests there have abundant subcanopial shrubs (*Chiliotrichum diffusum* and *Berberis buxifolia*). The field layer is composed of few grasses (*Bromus unioloides, Phleum alpinum*) and dicotyledoneous rosette herbs (*Osmorhiza chilensis, Calceolaria biflora, Ranunculus peduncularis, Taraxacum*). Bryophytes are generally very sparse in the woodlands, but species such as *Acrocladium auriculatum, Tortula robusta, Lophocolea bidentaa* and *Roivainenia jacquinotii* are characteristic.

Fig. 25. Woodland scenery, northern Península Mitre, showing an old *Nothofagus antarctica* stand. *Festuca gracillima* is rare in the eastern steppes, giving place to a mixed grassland lacking evident dominants. Moist meadows occupy the valleys. Photo: Sakari Tuhkanen (1987).

Fig. 26. Old *Nothofagus pumilo* forest in the relatively dry central part of the main island, with a sparse undergrowth due to the shadow of the tree canopy, and a troll forest atmosphere created by fallen stems covered by a soft carpet of mosses and beard lichens hanging from the branches. Photo: Sakari Tuhkanen (1985).

(Dusén 1903a, Holmberg 1906, Reiche 1907, Pisano 1977a, Moore 1983a). Collantes et al. (1989c) placed this vegetation into the Agropyro Nothofagion antarcticae alliance and Pisano (1977a) distinguished a Nothofagetum antarcticae association.

In Tierra del Fuego the woodland limit moved forth and back during postglacial times. There was a gradual extension of forest to their widest distribution once covering most of Tierra del Fuego with a later receding of the limit bringing it to the presente intermediate position. Auer (e.g. 1933a, 1939, 1958a, 1960) and Kalela (1941a, d) considered the regression as essentially driven by climatic drying, but this view has been challenged by Veblen & Lorentz (1988). There is not doubt that over-grazing, bush and forest fires, unsystematic wood-cutting and pasturing in he forest used to be harmful in whole Fuego-Patagonia (Eriksen 1972, Soriano & Movia 1986), but during the past few decades an expansion of trees into the steppe has been observed in some parts of Patagonia (Veblen & Lorenz 1988). The growth of the Río Grande town during the last century led to the obvious demise of ecotonal forests in its vicinity.

d. Deciduous forest

With increasing moisture the woodland gives way to a closed deciduous forest formed by *Nothofagus pumilio* (Fig. 26). Except in mountain forests and easternmost Fuegia, *N. pumilio* and *N. antarctica* grow only in separate stands. However, they often grow side by side forming forest islands with *N. pumilio* cores and *N. antarctica* margins. *N. pumilio* forests have closed canopies with light interiors but both shrub, field and ground layers show little diversity or actual coverage. There is plenty of acid slowly decomposing dry leaf litter that hinders the establishment of sedlings and the attachment of bryophytes. Acidic brown forest soils with the organic layer of moder-type are characteristic. Annual rainfall in the deciduous forest area of Fuegia is 450-650 mm.

Nothofagus pumilio has a limited but distinguished associate flora of its own including as foremost broad-leaved *Adenocaulon chilense, Macrachenium gracile, Dysopsis glechomoides* and *Viola* spp. Dry variants include also *Galium* spp. while mesic and coastal variants may possess richly *Berberis ilicifolia, Maytenus disticha* and *Gavilea lutea* stands. Except for *Berberis* which shows an affinity to evergreen communities of *Nothofagus betuloides* in more humid parts of Fuegia, the herbaceous associates of *N. pumilio* grow well in mixed evergreen-deciduous stands but diasppear from under dominant *N. betuloides*. (Dusén 1903a, Reiche 1907, Skottsberg 1909, 1916, Pisano 1973a, 1974, 1977a, McQueen 1976, Donoso 1981, Moore 1983a). Knapp (1966) places closed deciduous forests into the Valeriano-Nothofagion pumilionis and Collantes et al. (1989) into the Violo-Nothofagion pumilionis alliance. Oberdorfer (1960) presents Anemone-Nothofagetum pumilionis, Pisano (1977a) Nothofagetum pumilii and Collantes et al. (1989c) Mayteno-Nothofagetum pumilionis associations.

In stunded treeline scrubs both the deciduous *Nothofagus* sometimes form common vegetatively spreading stands of near equal life-forms and coverages. Mixed deciduous forest stands at low altitudes occur in eastern Península Mitre.

Lowland *N. pumilio* forests east of Lago Fagnano are relatively spaced but have broad canopies. Dry leaf litter is abundant and thus the undergrowth remains very sparse. Shrubs are lacking and only solitary individuals of *Cystopteris fragilis, Osmorhiza depauperata, Galium* spp. and *Acaena* spp. are found. A dense population of guanacos is responsible for the spread of *Galium* spp., *Stellaria media, Cerastium fontanum* and *Poa pratensis*. The characteristic mosses are *Acrocladium auriculatum* and *Lepyrodon lagurus*.

The Central and Marginal Cordilleran forests are relatively dense, generally with a single canopy. The forests of sheltered interior areas

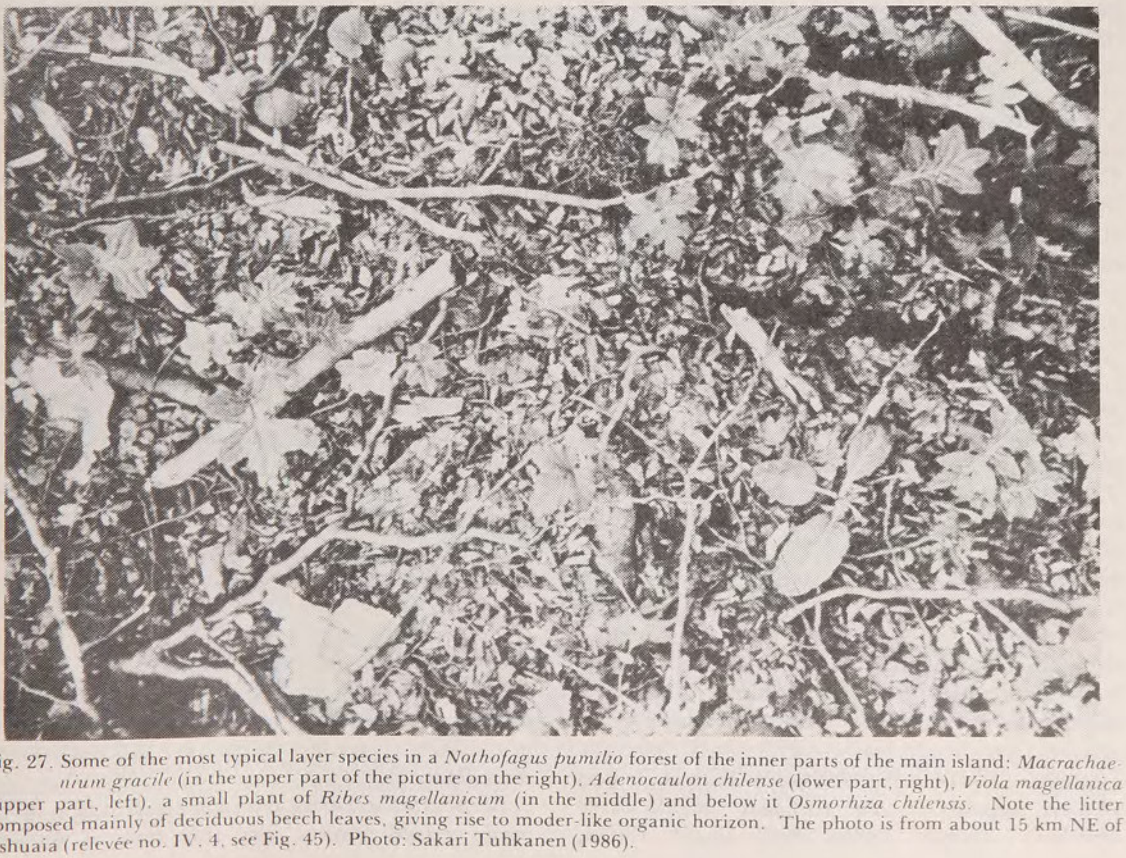

Fig. 27. Some of the most typical layer species in a *Nothofagus pumilio* forest of the inner parts of the main island: *Macrachaenium gracile* (in the upper part of the picture on the right), *Adenocaulon chilense* (lower part, right), *Viola magellanica* (upper part, left), a small plant of *Ribes magellanicum* (in the middle) and below it *Osmorhiza chilensis*. Note the litter composed mainly of deciduous beech leaves, giving rise to moder-like organic horizon. The photo is from about 15 km NE of Ushuaia (relevée no. IV. 4, see Fig. 45). Photo: Sakari Tuhkanen (1986).

have some *Ribes magellanicum* in the shrub layer while the communities with more direct exposure to the oceanic influence are often characterized by *Berberis ilicifolia*. In a diverse field layer *Rubus geoides, Viola magellanica, Dysopsis glechomoides, Adenocaulon chilensis* and *Macrachaenium gracile* are standard species (Fig. 27) while closer to the channels *Maytenus disticha, Pernettya mucronata, Senecio tricuspidatus* and *Gavilea lutea* must be added. The interior bryophytes are few including *Acrocladium auriculatum, Lepyrodon lagurus* and *Leptoscyphus expansus*. In moister aspects *Bartramia halleriana, Brachythecium* spp., *Platyneuron laticostatum, Rhizogonium mnioides* and *Adelanthus lindenbergianus* are also frequent.

The Cordilleran valley forests have commonly tall canopies and rich field layers. On Península Mitre where most lowlands are paludified, *Nothofagus antarctica* is a member of riverine forests. Along with the abundant herbs (*Osmorhiza* spp., *Viola magellanica, Dysopsis glechomoides, Adenocaulon chilense*) rare broadleaved grasses like *Agrostis leptotricha* and *Trisetum cernuum* plus a sedge *Uncinia lechleriana* are found. The shrub layer may be almost absent but bryophytes are numerous: *Acrocladium auriculatum, Lepyrodon lagurus, Chorisodontium leucopterum, Rhizogonium mnioides, Dendroligotrichum* spp. and *Adelanthus lindenbergianus* with a number of other hepatics.

e. Mixed deciduous-evergreen forest

Across south-central Tierra del Fuego, where annual rainfall is 500-900 mm, there is a narrow mixed forest zone with deciduous *Nothofagus pumilio* and evergreen *Nothofagus betuloides*. These are probably the most productive and lofty of all Fuegian forests with double canopies where the upper reaches 25-30 m, sometimes even almost 40 m. The soil characteristics of mixed forests resemble the brown podsolic soils of *N. pumilio* forests. Accordingly the associate flora is quite similar to deciduous communities, but *Hymenophyllum secundum, Luzuriaga marginata, Berberis ilicifolia* and *Codonorchis lessonii* are indicators of increased oceanic exposure. In the wet easternmost Fuegia *Drimys winteri* appears in the company of all three beeches. (Alboff 1896,. 1902, Dusén 1903a, Reiche 1907, Skottsberg 1909, 1916, Cozzo 1949, Holdgate 1961a, Correa Luna 1964, Pisano 1973, 1977a, 1983b, Kühnemann 1976, Dollenz 1982c, Moore 1983a, Veblen et al. 1983).

At low altitudes by the inner Fuegian channels relatively dry deciduous-evergreen forests are characteristic. Here *Drimys winteri* and *Maytenus magellanica* thrive under *Nothofagus* canopies. The former is characteristic but the hard-wooded *Maytenus* has been decimated from many places. In mature stands there is a dense scrub of *Berberis ilicifolia* while in open and successive communities *Embothrium coccineum, Fuchsia magellanica, Chiliotrichum diffusum* and *Discaria chacaye* are frequent. *The field layer is composed of Maytenus disticha, Adenocaulon chilense, Acaena ovalifolia, Osmorhiza* spp., *Gavilea lutea* and *Lagenifera hariotii*. In moister variants young *Drimys* and *Nothogafus betuloides* are common with *Luzuriaga marginata, Blechnum penna-marina, Viola magellanica* and *Dysopsis glechomoides*. Bryophytes show a clear affinity to woodland communities with *Bartramia halleriana, Brachythecium* spp., *Chorisodontium leucopterum, Platyneuron laticostatum, Tortula anderssonii, Adelanthus lindenbergianus* and *Lophocolea bidentata*.

Within the southern channels mixed lowland forests may be found together with evergreen communities. In eastern Península Mitre and Staaten Island both deciduous *Nothofagus* form communities with *N. betuloides* in strongly humid conditions (Cozzo 1949, Kühnemann 1976, Bianciotto 1986). Compared to most coastal forests of the Beagle Channel and Seno Almirantazgo the eastern forests have a rich and stratified undergrowth composed of both central Fuegian and archipelagic elements. The eastern mixed forests have commonly *Nothofagus pumilio* in the upper canopy with *N. betuloides* and *Drimys* filling both subcanopies, shrub and field layers. Together with the frequent *Hymenophyllum* spp. and *Lebetanthus myrsinites* taller broad-leaved herbs (*Polystichum multifidum, Senecio acanthifolius, Anthoxanthum redolens*) are found. In the ground layer mosses (*Dendroligotrichum dendroides, Dicranoloma australe, Rhizogonium mnioides*) surpass hepatics (*Gackstroemia magellanica*).

N. betuloides forms the natural climax state of many mixed forests, but this state is seldom reached and even then the field layers display affinities towards *N. pumilio* (Fig. 28). Because of shading canopies the undergrowth of an evergreen state is sparser than in the mixed state. Pisano (1977a) regards the deciduous-evergreen forests as Nothofagetum betuloidis pumilii association.

f. Evergreen forest

As the humifity is strongly increased together with the winter-moderating oceanic influence in the western archipelagic area, the evergreen *Nothofagus betuloides* becomes the dominant forest tree as there is less competition from *N. pumilio*. Annual rainfall is at aleast 600 mm, but may be even 3.000 mm. In some cases the distribution of deciduous beeches may be restricted rather by bedrock characteristics (igneous/sediment origins) than by climatic factors. The forest growth on sediment rocks in parts of the rainy eastern Fuegia may be excellent and a soaked peat layer has not developed. On poor impermeable rocks (schist, diorite) of the Coastal and Central Cordilleras continuous waterlogging leads to dense, monotonous swamp forests of *N. betuloides*. Here acid soils with heavy accumulation of peat develop.

In the archipelagic area, most of the soft-leaved herbs are absent and substituted by a thick sward of creeping *Hymenophyllum* spp., *Lebetanthus myrsinites, Luzuriaga marginata* and bryophytes (*Ptychomnion cygnisetum, Gackstroemia* *magellanica, Lepidolaena menziesii, Leptoscyphus horizontalis, Megaceros endiviifolius, Plagiochila bispinosa,* and *Schistochila lamellata)*. In the forest interior *Drimys* and *Berberis ilicifolia* are frequent but not abundant. Good drainage and additional light bring about more stratification: *Drimys, Pernettya mucronata, Philesia magellanica, Gleichenia quadripartita* (Fig. 29). In northwestern Fuegia *Pilgerodendron uviferum, Tepualia stipularis* and *Pseudopanax laetevirens* may apper as shrubs or small subcanopial trees. (Dusén 1903a, Hatcher 1903, Skottsberg 1909,

Fig. 28. Example of *Nothofagus betuloides* forest floor by the Beagle Channel. Seedlings of *Drimys winteri* with abundant *Codonorchis lessoni, Luzuriaga marginata, Blechnum penna-marina* and bryophytes can be seen. As a rule, all the subcanopy layers are better developed in the *N. betuloides* forests than in the drier *N. pumilio* forest. Photo: Sakari Tuhkanen (1986).

Fig. 29. In the southwest and west of the Fuegian archipelago rain forests occur in protected sites. The picture is from Isla Clarence. Photo: Sakari Tuhkanen (1987).

1916, Spegazzini 1923, Roivainen 1930, 1954a, Pisano 1970 a, b, 1971 a, b, 1971b, 1972a, 1973a, 1977a, 1983a, b, Young 1972, Crow 1975, Kühnemann 1976, McQueen 1976, Donoso 1981, Dollenz 1982b, Dudley & Crow 1983, Moore 1983a, Veblen et al. 1983). Evergreen forests are placed in the Nothofagetum betuloidis association by Oberdorfer (1960), Nothofagion betuloidis alliance by Knapp (1966) and Wintero-Nothofagetalia order by Collantes et al. (1989c).

Windward coastal scrubs with *Maytenus magellanica* and *Fuchsia magellanica* are restricted to the drier margin of the closed evergreen forest. Within the archipelagic channels *Pernettya mucronata, Berberis ilicifolia, Chiliotrichum diffusum* and *Philesia magellanica* become frequent. This vegetation is included in the Berberi-Escallonietalia order of Knapp (1966).

g. Oceanic moorland and scrub

Towards the western archipelagic area vascular cushion-plant bogs with scattered swampy woodland form a vegetation type termed oceanic moorland ("Magellanic moorland"; Godley 1960a, Moore 1979). Annual rainfall in this area is 1.500-4.500 mm. Continuous strong winds and very high cloudiness throughout the year are striking features of this extremely oceanic climate. In the outer archipelago closed forest communities practically disappear or they are developed only in a few sheltered coastal localities and on very steep leeward slopes. In the central archipelagic area all level land is covered by extensive bog landscapes, blanket bogs (hard *Astelia* cushion bogs and soft *Carpha* or *Schoenus* bogs) and on moderate slopes paludified woodlands prevail. In the outer islands drizzle and winds have washed steeper diorite rocks barren. There are fewer custhion bogs and swampy woodland when compared with more sheltered islands. On the shores the wind forces both *Nothofagus* and *Drimys* down to scrub contributing to impenetrable coastal thickets. Low scrub forests are found behind the coastal scrub in the exposed outer islands. (Dusén 1903a, Reiche 1907, Skottsberg 1916, Pisano 1972a, 1977a, 1980 a, b, 1982a, b, 1983a, b, McQueen 1976, Dollenz 1980, 1981, 1982a, Moore 1983a, Pisano & Venegas 1984). Knapp (1966) places the scrub forest into the Nothogagion betuloidis alliance, the archipelagic scrubs into the Berberi-Escallionetalia order, the epiphyte communities into the Dicranolomo-Hymenophy-

30.

llion alliance and the vascular cushion plant bogs into the Astelio-Oreobolion alliance.

The swampy woodlands of the archipelagic channels are formed of a sparse cover of deformed *Drimys* and *Nothofagus betuloides* with occasional groves of *Pilgerodendron uviferum*. There is a tall underscrub of *Pernettya mucronata, Berberis ilicifolia* and *Escallonia serrata* with *Philesia magellanica, Lebetanthus myrsinites, Empetrum rubrum, Gleichenia quadripartita* and *Hymenophyllum* spp. in the field layer. *Dicranoloma robustum, Blepharidophyllum densifolium, Gackstroemia magellanica, Lepicolea rigida, Leptoscyphus horizontalis* and *Schistochila* spp. are characteristic in the extremely rich bryophytic growth. Most of the trees and shrubs are wrapped by bryophyte, lichen and fern epiphytes.

In strongly windy expossed conditions, the bogs in the outer archipelago are formed by vascular cushion plants. The predominant constituent is *Donatia fascicularis* with additional *Astelia pumila, Oreobolus obtusangulus* and *Drosera uniflora*. *Pilgerodendron* is a frequent tree in the cushion bog communities, but stunted *Drimys, Nothofagus betuloides, N. antarctica* and *Embothrium* are also found. Shrubs are less common, but *Chiliotrichum diffusum* and *Gaultheria antarctica* are regular associates. In the lee of the outer islands wide monotonous Cyperoid bogs with high dominance of *Schoenus antarcticus* and *Carpha alpina* form the landscape.

Exposed outer archipelagic scrub woods are only lightly swampy contributing, to relatively dense stands. There is a single canopy of *Nothofagus betuloides* and abundant *Drimys* that lets light through. The scrub layer is dense and well-developed consisting of dominant *Desfontainia spinosa, Pernettya mucronata* and *Berberis ilicifolia* with *Escallonia serrata, Chiliotrichum diffusum, Blechnum magellanicum, Philesia magellanica, Lebetanthus myrsinites* and *Gleichenia quadripartita*. The exposed communities have relatively scarce epiphytic, field and ground layers. On islands with a low relief like Isla Noir the scrub forest may cover wider areas than the coastal rim (Pisano & Venegas 1984).

Thickets on windward shores are frequent in the archipelagic area. The conspicuous coastal scrubs around the outer islands are principally low scrub forests of which. *Drimys, Escallonia serrata* and *Hebe elliptica* are the most frequent constituents. Towards even more exposed sites (e.g. Cape Horn archipelago) *Drimys* disappears, *Escallonia* retreats to form scrub at higher altitudes and *Hebe* is left alone in the coastal community with *Poa flabellata* (Dollenz 1981, 1982, 1983a).

Isla Diego Ramírez about 110 kms SW of Cape Horn and Islas San Ildefonso west of Cape Horn display herbfield (*Plantago barbata, Ranunculus biternatus*) and coastal tussock grass (*Poa flabellata*) vegetation without woody species (Darwin 1839, Aubert de la Rüe 1959a, Pisano & Schlatter 1981a, b). This vegetation regime is not found in the main Fuegian archipelago, but it is characteristic of many desolate islands of the South Sea (Wace 1960, 1965).

h. Mires

Like vegetation in better drained sites the Fuegian mire types are arranged as a west-east sequence along the climatic humidity gradient (Auer 1963a, Alhonen & Auer 1979). The dichotomy between zonal and azonal vegetation vanishes in the archipelagic area as peatlands gradually become zonal vegetation. Roivainen (1954a) and Auer (1963a) distinguish three main classes of peatlands. Seasonally flooded vega grasslands without *Sphagnum* (Steppenmoore) are found in the valleys of northern and central Isla Grande coinciding with the steppe and a part of the woodland area (e.g. lower Río Grande system). Various *Sphagnum magellanicum* bogs (Sphagnummoore) characterize the Central and Marginal Cordilleran valleys including the upper Río Grande basin. In Tierra del Fuego *Sphagnum* bogs follow approximately the extent of *Nothofagus pumilio* forest. In the archipelagic area extensive rain region bogs (Moore des Regengebietes or Polstermoore) cover a large part of the land surface. Between the main mire types rather broad areas of transition exist. As noted by Roivainen (1954a) and Koponen (1971) many species of these and of other wet localities have bipolar distribution.

Fens and raised bogs are frequent in the area of deciduous and mixed forests (Fig. 30; Roivainen 1954a, Schawaar 1976, 1979, 1981). Sedge fens are young mires often along flooding rivers with dense beaver populations. They have

Fig. 30. *Sphagnum magellanicum* raised bogs with pools cover extensively the lowlands in central Península Mitre. Photo: Ilpo Kuokka (1985).

31.

abundant *Sphagnum fimbriatum* together with the common *S. magellanicum* and few vascular plants (*Carex magellanica, C. canescens*). Drier variants of rush fens are characterized by *Rostkovia magellanica*, the moister by *Marsippospermum grandiflorum*. Overgrown pools in dying centres of old raised bogs are characterized by *S. falcatum* and *Chorisodontium sphagneticolum*. *Tetroncium magellanicum* and *Sphagnum magellanicum* form an aggressive overgrowing community in the succession from fens to raised bogs. On fens with a flat profile and limited water supply, windiness may cease the growth of *Sphagnum* leading to hummock bogs of *Polytricum strictum*.

Roivainen (1954a) united all central Fuegian *Sphagnum magellanicum* raised bogs under a dwarf shrub tupe with *Empetrum rubrum*, *Pernettya pumila* and *Nothofagus antarctica*. Drier variants also include *Polytrichum strictum* and *Pseudocyphellaria freycinetii*. In the area of moister climates *Marsippospermum grandiflorum* and *Chiliotricum diffusum* are conspicuous in older bog communities that may, under the influence of heavy winds, have sloping instead of raised profiles.

Between the areas of *Sphagnum* bogs and archipelagic moorland several transitional types occur (Roivainen 1954a). Graminoid bogs of the rain region become dominated by tall *Marsippospermum grandiflorum* and *Festuca purpurascens*. In the young fens of the rain region hepatics, *Dicranoloma* spp., *Caltha appendiculata* and *Carpha alpina* are characteristic. If the rainfall or exposure is not excesive, the fens develop into raised bogs where *Chorisodontium magellanicum*, *Dicranoloma australe* and hepatics are important along with *Sphagnum*. *Empetrum rubrum* is the main vascular species, but stands of miniature sized *Nothofagus betuloides* and *N. antarctica* are also frequent.

Swamp forests become frequent in the area of deciduous-evergreen forests (Roivainen 1954a). Insufficient drainage causes the slowing of decomposition and accumulation of wet foliage where a *Marsippospermum grandiflorum*, *Chiliotrichum diffusum*, *Pernettya mucronata* community may become established. At lower altitudes the deciduous-evergreen forests develop in to mossy swamp forests (*Berberis ilicifolia*, *Chorisodontium* spp.) and into herbaceous swamp forests (*Anthoxanthum redolens*, *Gunnera magellanica*, *Acaena magellanica*) in the seepage drains of the mountain forests. At margins of expanding bogs, swampy *Nothofagus antarctica* edges are found. Roivainen (1954a) called wooded archipelagic communities swamp forests of the rainy region. In the inner archipe-

Fig. 31. Blanket bogs characterized by cushion plants occur in the relatively plain easternmost part of the main island (eastern Península Mitre) with abundant rainfall. Photo: Ilpo Kuokka (1987).

Fig. 32. Curved and twisted trunks in a krummholz forest near tree line. The effects of avalanches and sliding soil are clearly seen. The undergrowth is very scarce. Photo: Ilpo Kuokka (1986).

lago a herbaceous variant (*Viola magellanica, Lagenifera nudicaulis, Dicranoloma* spp., hepaticae) is distinguished, white towards the outer archipelago hepaticeous and fern-rich variants become more common.

Roivainen (1954a) distinguished two variants of the cushion bogs of the rainy region: a level type (Fig. 31) and a hummock type. The former consists of an aggregate of hard vascular plants (*Astelia pumila-Donatia fascicularis-Oreobolus obtusangulus)* with creping dwarf shrubs (*Gunnera lobata, Myrteola nummularia*). The hummock type is formed of hepatics, *Chorisodontium magellanicum* and *Racomitrium willii.*

i. Montane forests and the upper tree-line

The upper tree-line in Tierra del Fuego is formed by the two decidupus *Nothofagus* species. On wind exposed sides there is seldom an abrupt limit between forest and alpine zone because both trees evolve gradually down to scrub. Lee sides, on the other hand owing to the strong accumulation of snow have sharp ecotones (Fig. 32). The oscillation of the temperature about th freezinf point leads to the creeping of snow or avalanches. The tree-line in Tierra del Fuego is generally found at the altitude of 500-650 m' depending on relief, wind and snow conditions. In good shelter *Nothofagus* scrub ("Krummholz") reaches 750 m in the Central Cordillera (Fig. 33). Although individual scrub clones may occur above the tree-line, mountain woodlands are not found. The wind makes the canopies of the upper forests very dense, but the undergrowth becomes sparse, especially by the disappearance of shrubs. Toward the south and west the tree-line becomes lower and indistinct, and is formed even by *Nothofagus betuloides.*

The deciduous mountain forests of the Central and Marginal Cordilleras are moister than their lower counterparts showing good growth. Shrubs are generally absent, but the field layer may be richly herbaceous with *Hamadryas magellanica, Osmorhiza chilensis, Dysopsis glechomoides, Viola magellanica, Pernettya pumila, Schizeilema ranunculus* and *Uncina lechleriana.* Frequent bryophytes include *Acrocladium auriculatum, Brachythecium subpilosum, Chorisodontium leucopterum, Platyneuron laticostatum* and *Leptoscyphus expansus.*

There is most probably a considerable increase in humidity with altitude in the forests of the channels. The field layer has fewer herbs than the coastal forest, but *Maytenus disticha, Codonorchis lessonii, Macrachaenium gracile, Gunnera magellanica, Rubus geoides* and *Hymenophyllum secundum* are characteristic under shading canopies. The frequent bryophytes show a dominance of hepatics (*Adelanthus lindenbergianus, Chiloscyphus hookeri, Lepidozia chordulifera,* and *Marsupidium urvillaneum*) and mosses of moist communities *(Chorisodontium leucopterum, Dicranoloma australe, Rhizogonium mnioides).*

In the easter Central Cordillera, are isolated evergreen mountain forests between the altitudes of 200 and 400 m. Direct oceanic exposure on the southern slopes of Sierra Beauvoir, for example, maintains distinctive interior evergreeen forests. A soft organic layer of undecomposed wood and leaf litter is formed

Fig. 33. A landscape from the valley of Tierra Mayor (valley of Río Lashifashaj) NE of Ushuaia. The bottom of the valley is extremely paludified, which is partly due to flooding caused by the abundance of introduced beaver. At the upper limit of the forest, krummholz is encountered. Above the krummholz floristically rich mountain meadws prevail up to 800 m. Certain vascular mountain species may reach well over 1.000 m in screes. Photo: Sakari Tuhkanen (1985).

despite the lack of waterlogging during most or the summer. The forest structure reminds that of the interior deciduous forests, but the compositions of species is somewhat different (*Nothofagus betuloides*, its own seedlings and scrub, *Rubus geoides*, *Chorisodontium leucopterum*, *Adelanthus lindenbergianus* and *Marsupidium urvilleaneum*). At higher altitudes and on exposed ridges the interior evergreen forest grades into a stunted form with heath-like underscrub (*Pernettya mucronata*, *Empetrum rubrum*).

Eastern Península Mitre is well-exposed to humid air masses and the mountain forests are predominantly evergreen while deciduous forests occur in valleys. The East Fuegian mountain forests resemble the exposed mountain forests of the central Beagle Channel area. However, on Península Mitre such humidity indicators as *Pernettya mucronata*, *Marsippospermum grandiflorum*, *Hymenophyllum* spp., *Dicranoloma robustum*, *Chiloscyphus hookeri*, *Clasmatocolea rigens*, *Marsupidium urvillaneum* and *Telaranea plumulosa* are frequent.

There is little data on the mountain forests in the area of igneous rocks in the southwest. The upper limit of *N. betuloides* is about 250 m in the south (Dollenz 1980, 1981, 1982a). On Isla Clarence windward scrubs rise higher than that. In the Cape Horn Islands *N. antarctica* forms frequent montane forests and scrubs between 330-420 m (Dollenz 1980, 1981, 1982a) but the species is infrequent and confined to bogs on for example Isla Clarence and Islas Furia.

j. Alpine vegetation

In the mountains in the forested area of Tierra del Fuego, the upper timber-line forms a marked physiognomic boundary between the forest and the "alpine" zone. Heaths, feldmark and fjell meadows are usually distinguished in the Fuegian alpine vegetation, the distribution and composition of which is determined by the physical nature of the substrate, availability of water and exposure to winds in addition to the altitude (Moore 1975).

In the inner cordilleras vascular cushion plant heaths with dominant *Bolax* hummocks or *Azorella lycopodioides* surfaces with additional

Fig. 34. Above the herb field on sliding clayey soil on a cerro north of the eastern part of Lago Fagnano. Dominant plants are the cushion-forming *Bolax* and *Hamadryas magellanica*. Photo: Ilpo Kuokka (1986).

Abrotanella emarginata are common on convex surfaces above timber-line. They host also often *Empetrum rubrum*, *Nassauvia magellanica*, *Acaena magellanica* and *Leucheria hahnii*. The round fjelds east of Lago Fagnano (Fig. 34) are covered by a mosaic consisting of *Azorella lycopodioides*, herbs with woody bases (e.g. *Senecio magellanicus*, *S. humifusus*, *Saxifraga magellanica*, *Drapetes muscosus*) and low grasses (e.g. *Deschampsia parvula*, *Poa alopecurus*, *Stipa rariflora*). In places *Empetrum rubrum* with some other dwarf scrubs (*Pernettya pumila*, *Myrteola nummularia*) may dominate the structure of communities. With increasing altitude and exposure the heath becomes impoverished, more open, and above the altitude of 800-1.000 m the scarce vegetation is made predominantly of small cushions of *Azorella selago* and *Saxifragella bicuspidata*.

In the high Central Cordillera and on northern Península Mitre (Sierra Noguera) the lower wind-sheltered alpine area may include rich meadows with *Chiliotrichum diffusum* and *Berberis buxifolia* shrubs and tall herbfields of *Senecio acanthifolius*, *Agropyron fuegianum* and *Anthoxanthum redolens*. Shorter *Taraxacum gilliesii*, *Tapeinia obscura*, *Agrostis meyenii* and *Phleum alpinum* are characteristic at more exposed sites.

In the Altos de Boquerón *Marsippospermum* seepage mires are found on the upper windward slopes and grass mires (*Alopecurus*, *Anthoxanthum*) on the leeward slopes. In the Central and Coastal Cordilleras mountain mires are composed of small mire plants (e.g. *Caltha* spp., *Viola* spp., *Nanodea muscosa*) that benefit from seepage. On Península Mitre extensive *Sphagnum-Marsippospermum* terrain bogs with scattered *Carex-Carpha* fens and *Caltha-Colobanthus* herbfields are found.

Feldmark, i.e. rock screes and areas of gently sloping terrain with talus deposits, may be extensive in the Fuegian high mountain country. Higher plants are few, which justifies the denomination "desierto andino" (Pisano 1974, 1977). Feldmark is characterized especially by dense lichen communities (e.g. *Usnea*). Towards the transition to cushion heaths *Nassauvia latissima*, *Saxifraga magellanica* and *Senecio humifusus* together with some low grasses (e.g.

Deschampsia parvula, Poa alopecurus and *Stipa rariflora*) may be common.

k. Late glacial and postglacial history of vegetation

The first pollen diagrams from Tierra del Fuego were presented by von Post (1929, 1931). Over several decades Väinö Auer (e.g. 1933a, 1958a) collected vast material on the vegetation history of Fuego-Patagonia. Especially due to Auer's several expeditions there exist more pollen diagrams from Tierra del Fuego than from any other part of South America.

Auer depended extensively on tephrachronology in the timing of strata distinguishing four volcanic ash layers in southern South America. Auer (1958a) assumed that Monte Burney in southern Chilean Patagonia was the sole volcano responsible for the ash tephras in the Magellanic area. Later he concluded that most of the volcanic activity in the Pacific area was rhythmic and synchronous with Fuegian events, thus making distinct tephras comparable (Auer 1974). Auer thought that deposits in the bog at La Misión, northwest of Río Grande, were laid dow during the whole 14.000 years after the peak of glaciation. This led him to believe that there was an early and rapid melting of ice and that refugia existed for the forest on the Pacific margin in front of the ice, and forest advanced as early as the late glacial period across the Cordillera.

Markgraf (1980a, b) radiocarbon dated Auer's La Mision material and thereby proved that the profile covered only 10.000 years. She assumed that the glaciations in both hemispheres were synchronous but the South American ice retreated somewhat later than northern ice caps and that there were no forest refugia in Fuegia (Markgraf 1983, 1987a, b), Heusser & Rabassa (1987), Rabassa (1987) and Heusser (1987a, 1989a, 1990) note periods of tundra vegetation (*Empetrum-Bolax-Acaena)* and temporary advances of *Nothofagus* during the early postglacial period (14.000-10.000 B.P.). During that time the climate was dry with alternating warmth. An archipelagic ice cap moved back and forth during that time. Then warm and dry conditions between 10.000-5.000 B.P. caused the spread of open *Nothofagus* woodland over most of Fuegia. But wetter and cooler conditions persisted in the cordilleran area since 5.000 B.P. leading to closed *Nothofagus* forest and mire communities. According to Moore (1983a) Tierra del Fuego was separated from the continent of South America at 10.000 B.P. and plants of the Magellanic moorland probably had refugia in Fuegia proper.

Using the La Misión profile as a baseline and assuming synchronous tephras Auer (1933a, 1958a) presented so-called isohylochrones for the advancement of both forest and woodland margins in Tierra del Fuego, rejecting an early carbon dating of the La Misión that did not confirm his scenario. They studies of Markgraf (1980a, b, 1983, 1987a, b) show postglacial changes from grassland with Magellanic moorland affinity, through a scrub phase, to a climatically favourable period at about 8.500 B.P. when *Nothofagus* appeared in the La Misión profile. There after the area was submerged for several millenia. After 5.000 B.P. woodland conditions persisted close to present time, when the woodlands suddently retreated. The La Misión area is today *Festuca* grassland. Another profile at Lago Yéhuin display woodland from 8.000 to 6.500 B.P. and a subsequent decrease in precipitation and forest until 5.000 B.P. Gradually a closed forest state was archieved by 3.000 B.P. Presently the area lies at the margin between forest and woodland. In northeastern Isla Clarence (presently closed *Nothofagus betuloides* forest) mixed forest prevailed at 8.000 B.P. Thereafter various evergreen communities have dominated in the area except for short deciduous spells at about 5.000 and 2.000 B.P.

IV. THE HISTORY OF EXPLORATION AND SCIENTIFIC, ESPECIALLY PHYTOGEOGRAPHICAL AND BOTANICAL,RESEARCH ON TIERRA DEL FUEGO

The southern extremity of South America, Tierra del Fuego, has been of great interest to various scientists. From a botanical point of view the history of the scientific research of Tierra del Fuego has been dealt by Soriano (1948), Godley (1965, 1970) who gives a good survey of the botanical research of the southern lands up to (1891), and Moore (1983a). Parodi (1961) examines the phases in the whole Argentine botanical research and Turril (1920) treats both Argentina and Chile in a very concise way. Castellanos (1945) surveys the botanical exploration in Argentina during the first half of the 19th century. Relatively comprehensive bibliographies are found in Castellanos & Pérez-Moreau (1941, 1944) about the botany in Argentina, in Moore (1983a) and Dudley & Crow (1983) about botanical works and in Bonarelli (1917) about earlier geological, geomorphological, climatological and botanical research in Fuegia. Dusén (1900) lists all the earlier expeditions to Tierra del Fuego. Useful summaries of earlier research are also given by e.g. Hooker (1847), Spegazzini (1896), Alboff (1896), Skottsberg (1916) and Martinić (1982) on botanical research, and Kranck (1932) and Auer (1970, 1974) on geological research. The history of discovery and exploration of the Magellanic region has been dealt with e.g. by Kohl (1876) in a detailed way, Martial (1888), Holmberg (1906), de Agostini (1924), Barclay (1926), Auer (1929), Riesenberg (1926), Hough (1971) and Martinić (1971). Moore (1983a) gives a list on vascular plant collectors in Tierra del Fuego: it seems that there are more than one hundred botanists who have studied flowering plants and ferns and left some trace of their activities in the literature or in herbaria Moore (1985) and Hässel de Menéndez et al. (1985) provide lists of vascular and cryptogamic collections from southern Patagonia.

1. Early records: the period from Magellan to the Napeolonic wars 1520-1790

The shores of the land now called Tierra del Fuego were for the first time sighted by Europeans from the decks of the Portuguese discoverer Ferdinand Magalháes convoy four hundred and seventy years ago, in the serene morning of October 21st, 1520 (Kohl 1876, de Agostini 1924, Grip 1928, Zweig 1938). About a month later after various escapades Magalháes and his convoy sailed to the open Great South Sea, the Pacific Ocean, from the All Saints Straits, which today bears his name, in his endeavour to find a sea route to India.

The British admiral Sir Francis Drake sailed in the Fuegian waters in 1577-78, and he was the first to make a map of Tierra del Fuego. Although he did not entirely circumnavigated the region, he supposed that Tierra del Fuego was an archipelago comprinsing a great number of large and small islands thus making questionable the earlier belief of an extensive continent round the South Pole, Terra Australis Incognita (Kohl 1876: 391-392) as Magellan already had (Grip 1928, Parry 1979). The first attempets of European inhabitants to colonize the region of the Straits of Magellan in a strategic sense were made during the 16th century, but they were doomed to failure (Auer 1929: 22-23, Canclini 1986).

In 1616 the Dutch sailors Willem Schouten and Isaac Le Maire rounded a rocky cape which they named "Het Kaep van Hoorn" after their ship ("Het Hoorn") (Kohl 1876: 442-445; see Fig. 35: Riesenberg 1940, Parry 1979). Thus another, stormy but wider pathway to the Pacific Ocean and at the same time to the western coast of the whole American continent and southeastern Asia was pioneered and open. The stream of navigators from Spain, England and Holland increased gradually, and Tierra del Fuego became well-known. The stimuli for the navigators were of commercial and strategic character, but observations of scientific significance were also made. Some of the navigators collected a few plants (e.g. John Winter, a vice-admiral in Drake's fleet, collected a specimen of a tree, later known as Winter's bark, *Drimys winteri*; Godley 1965: 141).

The earliest real collection of plants from the Magellanic region was made -as far as is known- by the surgeon George Handisyd in 1690 (Middleton 1909, Gunckel 1971). The collection, now located in the Bristish Museum, contains a number of very characteristic species for the region, e.g. *Maytenus magellanica, Philesia magellanica, Fuchsia magellanica, Gunnera magellanica, Osmorhiza chilensis, Luzuriaga marginata* and *Donatia fascicularis*, including the first gatherings of mosses and lichens, as well (*Racomitrium lanuginosum* and four species of lichens, determined as *Cladonia rangiferina, Stereocaulon ramulosum, Sticta pulmonaria, Cladonia sylvatica;* Middleton 1909).

The firts true naturalist to visit Tierra del Fuego was the French Philibert Commerson, specialized in ichtyology, on Louis Antoine de Bougainville's voyage round the world (Oliver 1909). When crossing through the Straits in 1767-68 he collected along the coasts, but almost exclusively on the Patagonian side. Commerson never returned alive to France, but his sketches and collections were forwarded to Paris. Commerson's collections, now at Muséum

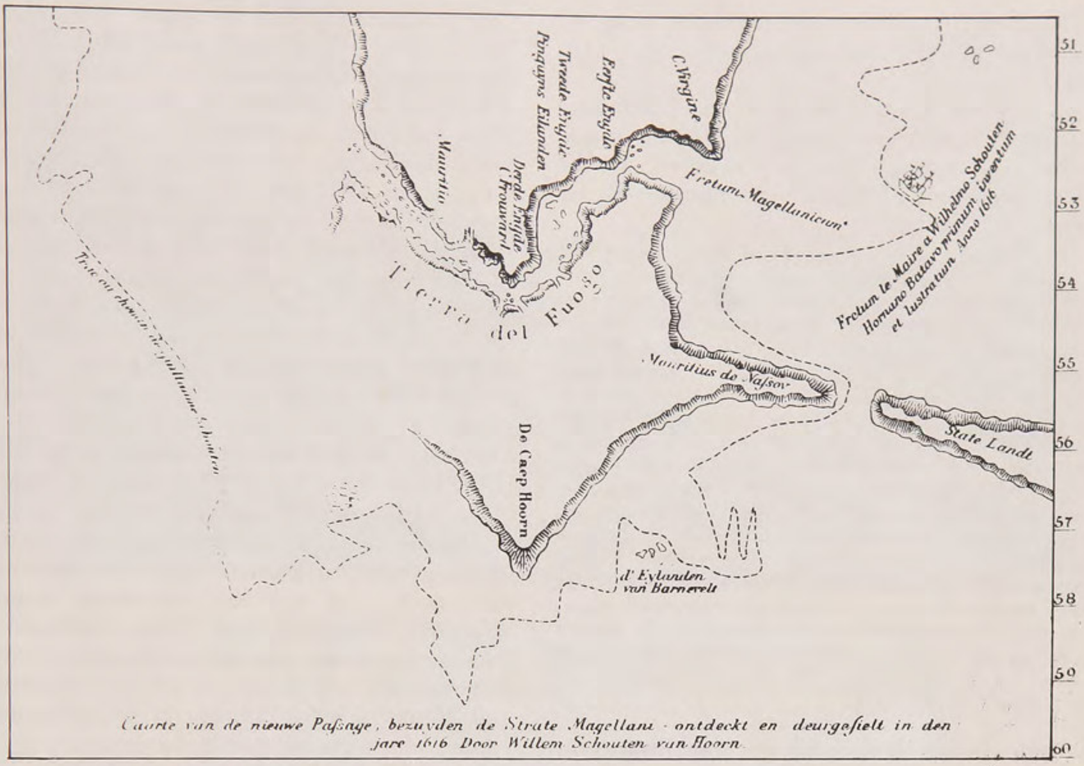

Fig. 35. Map of Tierra del Fuego based on Willem Schouten's and Isaac Le Maire's voyage in 1616. From Kohl (1976).

d'Histoire Naturelle in Paris, were the basis of botanical knowledge of the Magellanic region for some sixty years (Turrill 1920). Commerson, for instance, defined such new genera as *Hebe* and *Ourisia* (Godley 1965: 143), and his collections included such conspicuous moss species as *Polytrichadelphus magellanicus* and *Dendroligotrichum dendroides* (Cardot 1908). The first record of hepatics is that of *Jungermannia magellanica* collected also by Commerson (Geissler & Bischler 1987) de Bougainville himself in his narrative (1771, 1772, 1783) distinguished the main vegetational formations along the Straits: the eastern grasslands, the central forest region, the barren western region, and even depicted this sequence on a map.

From the scientific point of view of the exploration of Tierra del Fuego, James Cook's (Badger 1970) first southern journey (1768-1771) in His Majesty's barque Endeavour was to be of great significance directly or indirectly , (Merril 1954). Cook landed at Bahía Thetis in the eastern tip of Isla Grande, and the first noteworthy collection of plants from the actual Tierra del Fuego was made at this place. The original reason for the voyage of Cook was astronomical, to make observations of the transit of Venus across the disc of the Sun, although it yielded little of astronomical value (Stern 1968, 1969).

Cook had two botanists with him, the good friends Mr. Joseph Banks and Dr. Daniel Solander, a Swedish naturalist, settled in England. Solander was a former student of Linnaeus, who in this way started the long-lasting and renowned Nordic research tradition in Tierra del Fuego. Cook's and Bank's journals of the voyage have been edited and published in their entirety (Beaglehole 1955, 1962). Solander did not probably keep any journal (Britten 1906).

After Bahía Thetis the Endeavour continued to Bahía Buen Suceso (Good Success Bay). On January 16th 1769 Banks and Solander went inland with a party of ten people in order to make an excursion to the top of near-by hills. This notorious excursion proved fatal to two men in the party, and nearly so to Solander as they were caught by a severe snow storm (in midsummer!), and the party was forced to spend the night in the open (Beaglehole 1962: 218-221).

In spite of misfortunes Banks and Solander managed to make collections of alpine, coastal and other plants, and they were satisfied with the collections made at Bahía Buen Suceso. Banks wrote:

> "Of Plants here are many species and those truly the most extraordinay I can imagine, in stature and appearance they agree a good deal with the European ones only in general are less specious, white flowers being much more common among them than any other colors. But to speak of them botanicaly, probably No botanist has ever enjoyd more pleasure in the contemplation of his Favourite pursuit than Dr. Solander and myself among these plants; we have not yet examind many of them, but what we have turnd out in general so intirely different from any before describd that we are never tird with wondering at the infinite variety of Creation, and admiring the infinite care with which providence multiplied his productions suiting them no doubt to the various climates they were designd. Trees here are very Few, Birch *Betula antarctica [= Nothofagus betuloides]*, Beech *Fagus antarcticus [= Nothofagus antarctica]*, winters bark *Winterana aromatica [= Drimys winteri]*, the two first for timber the other for its excellent aromatick bark so much valued by Physicians are all worth mentioning;..." (Beaglehole 1962: 225-226).

From Bahía Buen Suceso the Endeavour continued round Cape Horn and entered the Pacific. This voyage started a period of some 80 years when almost all botanical exploration was concentrated on the Beagle Channel region, Staaten Island and southwards through Isla Wollaston. The Endeavour voyage led to many other subsequent, significant voyages (the Forsters on the Resolution, A. Menzies on the Discovery, C. Darwin on the Beagle, etc.).

Banks and Solander collected nearly 150 specimens in Tierra del Fuego (including many mosses and lichens) of which about one hundred were new, among them *Berberis ilicifolia* and *Perezia magellanica* (Britten 1905, Stearn 1968: 7). The specimens collected by Banks and Solander as well as the botanical results of the voyage of Cook are discussed by Arber (1945), Groves (1962) and Stearn (1968, 1969). The specimens are held in the herbarium of the British Museum, and they are mostly in good condition (Groves 1962: 59).

Banks' and Solander's collection is superb, but they failed to carry their results to the point of publication (Arber1945) Solander (s.a.) prepared a manuscript concerning Tierra del Fuego, "Primitiae Florae Terrae del Fuego sive Catalogus Plantarum prope Fretum le Maire A. C. MDCCLXIX diebus 14-20 Jan. collectorum", but is was never plublished. This is, very regrettably, characteristic of Solander. Many important findings made by them seem to have been published by others (e.g. the Forsters), probably in some cases without any reference to him (Fries 1940:295, Merrill 1954:200). Sir Joseph Banks was regarded as a patron of science rather than a man of scientific attainments, but, in fact, he had much botanical knowledge (Britten 1905, Cameron 1952). Like in the case of Solander many of his designations were published or attached to other persons' names (Arber 1945). In any case, Banks and Solander made a fundamental contribution to he knowledge of the flora (and fauna) of the world (Fries 1940, Rauschenberg 1968, Stearn 1968).

Daniel Solander passed into memory in 1782 and by the time of Bank's death in 1820, the days of the gentleman amateur dilettante in science were over. In addition, systematic botany, Solander's speciality, was being displaced as botany moved into new ultimately more productive channels. All in all, the world of Solander's and Banks' science passed on (Rauschenberg 1968). The scientific milieu changed.

Cook's second voyage was his greatest navigation, which was to revolutionize knowledge of the Southern Hemisphere (Godley 1965: 146). On this voyage in 1772-75 by the Resolution and Adventure, there were two incorporate botanists, Johann Reinhold Forster and his son, Johann Georg Adam. They were also joined by Anders Sparrman, a Swedish pupil of Linnaeus. Cook's original journal of the voyage (1777) has later been edited and republished by Beaglehole (1961). Also G. Forster (1777) and A. Sparrman (1802, 1953) kept and published their own journals.

In Tierra del Fuego collections were made at two places in 1774-75: at a place called Christmas Sound (Canal Navidad) by Cook, located on a desolate coast of the Beagle Channel on Isla Hoste, and off the northern coast of Staaten Island on Isla Año Nuevo. The Forsters and Sparrman investigated especially the forest vegetation (Turrill 1920).

The Forsters seem to be the first naturalists who published botanical records from Tierra del Fuego other than the usual ship journals in scientific periodicals: they described new genera and in detail the collections from Tierra del Fuego (J.R. & G. Forster 1776, G. Forster 1789).

Fig. 36. "We continued our course into the bay, and entered the second opening on its western side, named St. Martin's Cove. Here all the beauties of the wildest Alpine scenery bust upon our view. As we passed into the cove, a wigwam was discovered, and smoke from wihich was curling among the trees. (...) During a few days after our arrival, we were much gratified with the company of some Fuegian people, as the natives of Tierra del Fuego are called (...). The vegetation of Hermite Island. The beech-tree is generally smaller, and appeared to be much stinted in its growth by the violence and constancy of the winds to which it is exposed. The antarctic or evergreen beech (a misconception: antarctic beech = *Nothofagus pumilio*, does not occur on Hermite Island; evergreen beech, *Nothofagus betuloides*, occurs there) is mingled with the deciduous species of this tree (*Nothofagus antarctica*). It was very scarce at Staaten Island; but here it grows in abundance. (...). The smaller scrubs, lichens, and plants were precisely the same as those we found at Staaten Island". Webster (1934: 173-174, 186-187).

The Forsters' specimens are now scattered through at least 12 herbaria (Carolin 1963, Merrill 1954: 208-211) the largest proportion being probably at Kew (cf. Britten 1885).

Archibald Menzies, a surgeon on a voyage of commercial discovery, collected at New Year Harbour (Puerto Año Nuevo) on Staaten Island in 1787 (Godley 1960b). The collection included some bryophytes described by Bescherelle (1889).

In general, the end of the 18th century and the beginning of the 19th were a quiet period in the scientific exploration of Tierra del Fuego. The Falklands, for instance, were visited more frequently (e.g. Malaspina and Née in 1789, Freycinet and Gaudichaud in 1817-20; see Godley 1965: 150-152).

2. A step forward. The great captains (1825-1840)

About a half century was to pass before any significant progress was made in the exploration and study of southern South America. The three great maritime nations, England, France and Spain, were heavily engaged in the Napoleonic wars. When peace came, the scientific exploration in many fields, in geography, geology, botany and zoology, started with vigour.

A trilogy (King, Fitzroy, Darwin; all three appeared in 1839) edited by Fitzroy is a monumental narrative on an important stage in the history of the exploration of the southern lands. The first of the three (King 1839) covers the surveying voyages of the two ships, the Adventure (Commander Philip Parker King) and the Beagle (Commander Pringle Stokes; after his suicide Robert Fitzroy) and their attendant smaller vessels during a period of three and a half years, from December 1826 to August 1830. James Andersson sailed on the Adventure as botanical collector. King's narrative as well as Fitzroy's and Darwin's include valuable observations of vegetation and geology. Also King's paper (1832) included very competent observations of the nature of the Magellanic region.

The coasts along the Strait of Magellan were surveyed and explored. Seno Skyring and Seno Otway were discovered by Fitzroy. The Adventure spent several weeks at St. Martin's Cove on Isla Hermite near Cape Horn. The Beagle surveyed the southern coast of Tierra del Fuego from the western entrance of the Strait of Magellan to Península Mitre (Bahía Buen Suceso) and the Beagle Channel was discovered in its entirety.

The collection made in the Magellan region comprised 167 specimens (almost as many species, mainly of flowering plants with a few cryptogams, and it was the most complete collection so far (Godley 1965: 157). But it covered only few localities, most gatherings were made at Puerto Hambre (Port Famine) on the Patagonian side. The collection was later of great value to Hooker in preparing Flora Antarctica.

The surgeon W.H.B. Webster was responsible for the natural history observations during the voyage of the Chanticleer in 1828-30 (Captain Henry Foster). The Chanticleer visited Staaten Island and Isla Hermite on her way to Deception Island, Antarctica. On her return the Chanticleer spent two months at St. Martin's Cove on Isla Hermite with the Adventure (see Fig. 36). Webster made only afew collections, but gives descriptions on the vegetation and other environmental conditions and on indigenous peole in his narrative Webster (1834).

One of the real pioneers of the natural history of Antarctica, James Eights, stopped at Staaten Island on his way to the South Shetland Islands (Calman 1937). He made some botanical collections there, but of more value were probably his zoological collections and observations.

In November 1831, Captain Fitz Roy left England again as commander of the Beagle. This time the young Charles Darwin was taken along "to examine the land". The objective of the voyage was to complete the survey of Patagonia and Tierra del Fuego, commenced under Captain King in 1826 to 1830. Narratives of the voyage, the second and third part of the trilogy mentioned above, were written by Fitzroy (1839) and Darwin (1839 and e.g. 1872, 1921). Captain Fitz Roy was one of those devoted naval officers-like de Bougainville, King, Foster, and Dumont d'Urville- who through their interest in science contributed so much to the knowledge of the southern lands (Godley 1965: 156).

In December 1832 the Beagle landed at Bahía Buen Suceso, and Darwin penetrated some way inland. He wrote about the forest which covered the terrain as follows:

> "The view was imposing but not very picturesque, the whole wood is composed of the antarctic Beech *[Nothofagus betuloides]* (the Winter's bark *[Drimys winteri]* & the Birch *[Nothofagus antarctica]* are comparatively rare). This tree is an evergreen, but the tint of the foliage is brownish yellow: hence the whole landscape has a monotonous sombre appearence; neither is it often enlivened by the rays of the sun [...] The number of decaying & fallen trees reminded me of the Tropical Forest. But in this still solitude, death instead of life, is the predominant spirit. The delight which I experienced, whilst thus looking around, was increased by the knowledge that this part of the forest had never before been traversed by man [Indians were usually not considered as human beings]". (Darwin's diary, December 19th 1832: Barlow 1934: 121-122).

Darwin also climbed the mountain which was visited by Banks and Solander about 60 years earlier. He was able to collect alpine plants, but the collections were rather small.

Later the Beagle visited St. Martin's Cove on Isla Hermite, Isla Navarino and some other places in the region of the Beagle Channel. After winter in Montevideo the Beagle returned to the Strait of Magellan. She surveyed the area for one month, then sailing through Estrecho de Le Maire to the southern parts of Tierra del Fuego, where she made several landings. After a visit to the Falklands the Beagle returned to the region of the Strait of Magellan, continuing finally to to Valparaíso in 1834.

Darwin gathered plants, although not to a great extent. The collections, now in the Royal Botanic Gardens, Kew, were used in the preparation of the Flora Antarctica by Hooker. In addition to botanical collections and observations, Darwin had many responsabilities in geology and zoology (Godley 1965: 164). In any case, Darwin and Captain King a few years earlier were among the first who made scientifically valuable and competent observations on the geology and geomorphology of Tierra del Fuego (see e.g. Darwin 1842: 417-423, 1906).

In 1837 J. Dumont d'Urville was ordered to sail under the French flag as far south as possible in the region of the sea which Weddell has discovered in 1823. Two corvettes, the Astrolabe and the Zélée sailed to the southern sea. In December and January 1837-38 the Astrolabe sailed in the Strait of Magellan. The offical narrative was written by Dumont d'Urville (1840, 1841-46). The surgeon Jacques Hombron was responsible for botanical collecting on the Astrolabe. The cryptogams collected were studied by Camille Montagne (1845) and the information was included in the Flora Antarctica. Beautiful plates of flowering plants and ferns were prepared and published under Hombrons edition (Hombron & Jacquidot 1853, see also Jackson (1888), but no text had been written by the time of Hombron's death in 1852. J.F. Decaisne (1853) filled this gap. The species list from Tierra del Fuego comprised, however, only some tens of species.

The second United States Exploring Expedition departed under the command of Charles Wilkes in 1838 towards the southern seas with the aim to promote the interests of commerce and navigation. Wilkes (narrative published 1856), however, also wanted to promote science, and finally he was provided with several naturalists. The ships of the fleet visited various parts of Tierra del Fuego in February-March 1839. Bahía Orange (Orange Harbour) on Península Hardy of Isla Hoste was one of their major ports. The botanist of the voyage was William Rich assisted by W.D. Brackenridge. Compared to the time at land and the number of naturalists, the collections cannot be considered as large: they comprised only 59 specimens from Tierra del Fuego (Moore 1983a). J.D. Dana (1854) was responsible for geological observations.

The results of the expedition were published in a series of volumes between 1846 and 1874. Asa Gray, who did not himself participate in the voyage, wrote the text for the volume on Phanerogamia (1854; atlas of plates 1856), and William D. Brackenridge completed a volume on Cryptogamia (ferns) in 1854 (atlas of plates 1855). A group of contributors prepared a volume on lower cryptogams which was published in 1874 (Collins 1912).

Godley (1965: 172) concluded that this American expedition like the French led by Dumont d'Urville suffered not having a first class botanist with them. The collections made were very small and great difficulties emerged as regads publication of the results, a very characteristic feature to many expeditions of those days (and subsequently!). But a remarkable exception was to come...

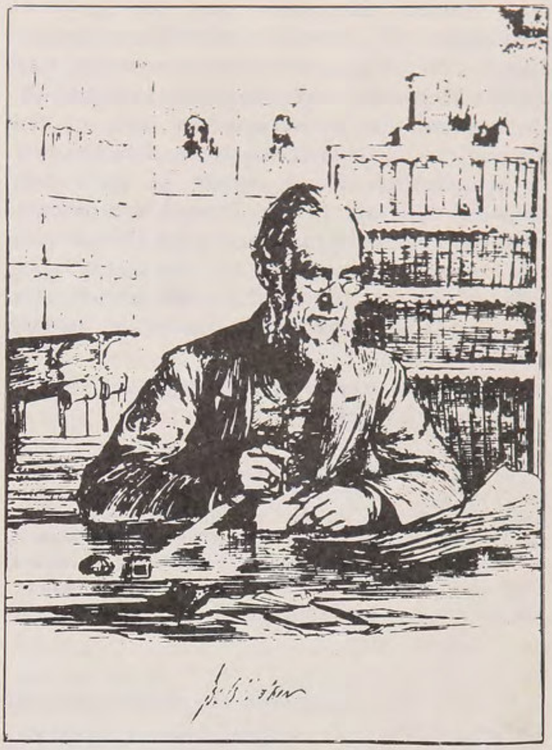

Fig. 37. Sir Joseph Dalton Hooker (1817-1911) in his study at Sunningdale, 1886, a few months after his retirement as director of the Royal Botanic Gardens, Kew. Turrill (1953: plate 21).

3. Joseph Dalton Hooker and the Flora Antarctica-cornerstone in the botanical research of the southern lands (1840-1850)

A British expedition left England in September 1839 with two ships, the H.M.S. Erebus (commanded by Captain Sir James Clark Ross) and the H.M.S. Terror (Captain F.R.M. Crozier). The assistant surgeons J.D. Hooker (Fig. 37) and David Lyall to take care of botanical observations and collecting. Robert M'Cormick and John Robertson, surgeons, were responsible for zoological and geological collections. The narratives were written by Ross (1847; include a plant-geographical account by Hooker) and M'Cormick (1884).

The voyage was directed to the Falklands and Tierra del Fuego, Kerguelen, Auckland Island and Franklin Island. This was the first of Hooker's important botanical expeditions (Turrill 1953: 134). Although he was a taxonomist in the first place, Hooker was, in fact, more interested in the general phytogeography, especially on problems of plant distribution, of the whole southern ocean area than in Tierra del Fuego and its flora themselves. He covered the moist southern side of the Fuegian archipelago (Cape Horn, Isla Hermite at St. Martin's Cove), where he spent two months. Although Hooker limited his studies to southern Fuegia, he managed to list 153 vascular species (but collected only 39; Moore 1983a), a third of the total native flora now known. He also listed and collected numerous mosses (Hooker in Ross 1847).

Hooker (in Ross 1846: 288) compared Isla Hermite to the West of Scotland:

> "The scenery of Hermite Island so closely resembles that of many parts of the West of Scotland, that the two countries seem only to differ in the species of animals and plants which respectively characterise the northern and southern hemisphere. There are the same narrow arms of the sea, confined by high mountains, in Hermite Island, as form the salt-water lochs of Argyleshire; [...]"

He describes changes in the vegetation from the sea shore up to the hill tops, and makes, among other thing, the following parallell (perhaps not very successfull) with Scotland:

> "The three trees, above described [evergreen southern beech, Fagus Forsteri i.e. *Nothofagus betuloides;* deciduous southern beech, Fagus Antarctica i.e. *Nothofagus antarctica;* Winter's barck, *Drimys winteri*] occupy exactly the same positions in Fuegia which the birch, oak and mountain ash do in Scotland". (Hooker in Ross 1847: 289-290).

On basis of the results of this voyage and other collections made earlier (especially the unpublished collection of Banks and Solander and Menzies), a cornerstone in the history of botany of Tierra del Fuego was to be created. The whole earlier style -collections but no scientific publications- was to be changed.

Sir William Hooker, Joseph's father, a very renowned botanist, too, oulined the plan of the great "Botany of the Antarctic Voyage" W.S. Hooker (1844). This monumental scientific publication on the southern lands consisted of three main portions: I Flora Antarctica, II Flora Novae-Zelandiae and III Flora Tasmaniae (see Jackson 1912 and Wiltshear 1913 concerning the actual dates of publication and the pagination of each monthly number). The second part of Flora Antarctica was "Botany of Fuegia, the Falklands, Kerguelen's Land, etc"...It appeared in fifteen numbers in 1846 and 1847. Hooker and various collaborators described the cryptogams in another series of papers (e.g. J.D. Hooker & Wilson 1844, J.D. Hooker & Taylor 1844) which were later included in the Flora Antarctica.

Hooker drew together all the scattered pieces of information published earlier, and added the results of his own gatherings and of the hitherto unstudied collections. A coherent picture of the botanical features on Tierra dle Fuego was crated. It was the first comprehensive summary of the Fuegian flora. Hooker believed "that successive expeditions have nearly exhausted the phanerogamic productions" of the Magellanic area. However, dozens of new species have been discovered since then.

The introduction to the second part of the Flora Antarctica (Botany of Fuegia...) includes general comments on Tierra del Fuego and the islands eastwards to Kerguelen comprising such matters as topography, climate, vegetation and earlier explorations. Amongst this information are to be found important generalizations concerning the geography of plants.

The connections between the floras of New Zealand and South America, their past histories, their origins and their migrations intrigued Hooker's mind (Turrill 1953: 229). He was the first to get the idea of an Antarctic origin and dispersal of the floras of the southern lands and paid attention to circum-antarctic connections. In the introductory essay to his Flora Novae Zelandie Hooker (1853) provided the theory that all the different groups originated and subsequently dispersed in the southern hemisphere on a continuous tract of land. This was no doubt the simpliest possible explanation for a major biological problem, but Hooker's theory was unacceptable to many of his contemporaries (Humphries 1985: 336). Darwin for example, could not agree with Hooker; he was influenced by stable earth theories and supported multiple origin theories with long-distance dispersal events (Humphries 1985: 336).

These introductory essays in the "Botany of the Antarctic Voyage" are classic and of very great value. They are syntheses of the then known facts, many of which were first discovered by himself. While his conclusions may now need a number of modifications, none of the major ones is entirely out of date and some have been widely or even completely acceped (Turrill 1953: 229).

The Hookerian publications dealing with not only the southern lands, but also with so many other themes, range in time from 1844 to 1904, and thus extend over a period of 60 years (Turrill 1953: 220). It was a period of industrial and scientific progress, of peace and of relative wealth.

4. Frequency of expeditions increases. Chile and Argentina start their own explorations of austral regions (1850-1890)

After Hooker's Flora Antarctica there was a more or less quiet spell of about four decades in the scientific exploration of the southermost part of South America Botany and geology remained mainly an incidental field of activity to scientists visiting Tierra del Fuego.

Williabald Lechler collected and listed some plants on the coasts of the Strait of Magellan in 1852-53, although he mainly collected on the Falklands and in the more northern regions of Chile (Gunckel 1948). In Plantae magellanicae (1857) he listed 53 florwering plants and a few cryptogams. Lechler's material from southernmost Patagonia was used by Grisebach (1854) and Schulz Bipontinus (1855).

Although several meritorious Swedes had visited Tierra del Fuego before, it was not until 1852 that the first truly Swedish expedition was realized. The voyage of the frigate Eugenia was mainly concerned with the expanding Swedish trade on the west coast of America, the East Indies and China, but physical and biological observations were also made. The botanist of the voyage was N.J. Andersson. His narrative (1853-54) includes accounts of the Strait of Magellan, but they do not contain any thing essentially new from a scientific point of view. The plant specimens collected by Andersson, only from the Patagonian side of the Strait have been widely distributed, and nothing has been published on the higher plants (Godley 1970:71). The bryophyte collection was studied by Angström (1872).

The aim of the voyage of H.M.S. Nassau in 1866-69 was to continue the survey of the Strait of Magellan and the West Patagonian channels commenced by King and Fitz Roy. The naturalist of the expedition was R.O. Cunningham, whose fascinating narrative (1871a) offers a very good image of the voyage. Cunningham (1869, 1871a, b) gave, remarcks for example, on the general east-west sequence of the main vegetation formations in Tierra del Fuego. He vigorously collected both plants and animals at a great number of landings in Tierra del Fuego and southern Patagonia. However, he never published any systematic description of his collections (Soriano 1948: 445). Crombie (1877) studied the lichens of Cunningham's collection.

The circum-navigation of the world by H.M.S. Challenger in 1872-76 was concentrated mainly on deep-sea exploration, but also other scientific observations were made. In December 1875-January 1876 the Challenger sailed in the southwestern parts of Patagonia and Tierra del Fuego. The team of scientists was led by Prof. Sir C. Wyville Thomson, geologist. On board there where also three zoologists, John Murray, R. von Willemoes Suhm and Henry Nottidge Moseley. The masive official narrative was written by T.H. Tizard (navigating officer), Moseley, Buchanan (chemist and physicist) and Murray (1885). Moseley made botanical collections, but apparently nothing from the Strait of Megellan (cf. Godley 1970: 54, Moore 1983a). A summary of the scientific results of the expedition was published by Murray (1895).

The German S.M.S. Gazelle visited the Strait of Magellan in February 1876. The main emphasis of the voyage was to carry out oceanographic research and to deliver and support the German transit of Venus expedition at Kerguelen. Surgeon H. Naumann was responsible for plant collecting. Engler (1889) presented the botanical material from Tierra del Fuego. The collection comprised about 100 different species from Tuesday Bay (Bahía Martes) and Punta Arenas in the Strait. On basis of the material collected, C. Müller (1884) could increase the bryological records and Müller Argoviensis (1883) lichenoloigical ones from Tierra del Fuego, Hackel (1885) dealt with some grasses.

Paul Amedée-Ludovic Savatier, chief medical officer, directed his course to the same areas as the Nassau some years earlier, on board of the frigate La Magicienne in 1877-79. He published a general account of the voyage in 1880. His collections were described in the reports of the French expedition to Cape Horn (e.g. Franchet 1889). Savatier's private collection is preserved at Kew (Stapf 1909).

It was not until in the last decades of the 19th century that the Chilean and Argentine governments extended their exploration to their southern possessions. J.T. Rogers and E. Ibar visited southwestern Argentine Patagonia in 1877 (Ibar 1879, Rogers & Ibar 1880). Similarly, a Chilean expedition was sent to the Strait of Magellan and the Chilean parts of southern Patagonia in 1877. Enrique Ibar Sierra collected mainly plants and birds for the National Museum in Santiago (Pisano 1977b). The taxidermist Pablo Ortega was sent by the same museum on the 1879 expedition of Lieutenant R. Serrano Montaner, whose discovery of gold in northern Isla Grande led to a gold rush (Martinić 1976).

In the 1880's, when the exploration of the southern parts of South America was vigorously intensifying, La Expedición Austral Argentina on board the corvette Cabo de Hornos was sent to explore the coasts of Patagonia and Tierra del Fuego in 1882 under the leadership of Giacomo Bove. His narrative was published one year later (Bove, 1833). The botanical work was taken over by Carlos Spegazzini, who represented the University of Buenos Aires. He collected extensively along the northern, western and southern coasts of Isla Grande, on a number of islands in the Canal Beagle and on Staaten Island (for a list of the collecting localities, see Spegazzini 1896). Spegazzini's findings (1896) upgraded substantially by about 160 species, compared to those known by Hooker, i.e. to about three quarters of those currently recognized (Moore 1983a).

Spegazzini's collections were also dealt with by other researchers: mosses by C. Müller (1885) who compiled a complete moss flora a Tierra del Fuego up to that time, describing 39 new species, lichens by Nylander (1888) and Müller Argoviensis (1889), and hepatics by Massalongo (1885). The gatherings increased the hepatic flora of Tierra del Fuego from 95 to 152 species. Spegazzini's collections are in the University of La Plata (Godley 1970: 78).

The geologist of the Bove expedition was Domingo Lovisato, who collected fossils. The results were published by Steinman (in Andersson 1907) and Hyades (1887).

John Ball (1887) traversed the channels of western Patagonia and the Strait of Magellan in June 1882. The winter season restricted his possibilities to gather plants. However, he made some collections, which are now at Kew (Godley 1970: 76). He was the first who proposed the phytogeographical term "Magellanic Province" (1886).

An Italian ship, the corvette Caracciolo (Captain Carlo de Amezaga) sailed trhrough the Strait of Magellan and in the west Patagonian channels in 1882 during her voyage round the world. Amezaga's narrative was published in 1885. It contains a general list of collected plants, but the collections were not large. A contribution to the lichen flora on the basis of the material collected was made by Jatta (1890).

Another Italian ship, the corvette Vettor Pisani also sailed in the Strait of Magellan and in the Patagonian channels in 1882 during her circum-navigation of the world (Chierichia 1884). Marine zoological collections were made. Probably the only plants collected were algae (Piccone 1886).

A notabel scientific contribution was to come during the French part of the Internaional Polar Programme of 1882-83. The expedition, "Mission scientifique du Cap Horn", led by Captain L. F. Martial on the Romanche from Cherbourg surveyed the coasts of Tierra del Fuego in order to make biological collections and observations on ethnology astronomy, meteorology and magnetism (see Martial 1888). A well equipped research station with pre-fabricated buildings and a photographic laboratory (Fig. 38) was erected for a party of 21 persons at Bahía Orange on the Península Hardy, southeastern extension of Isla Hoste.

Dr. Paul Hyades, Mr. Paul Hariot and Dr. Philippe Hahn made biological and geological collections int he vicinity of Bahía Orange using the mission-station as a base, but sailed also in different parts of Tierra del Fuego, mainly in the archipelago south of Isla Grande. Very precise meteorological observations were made at the station in Bahía Orange, which are still the only available ones from Isla Hoste. The surveying in the southern archipelago produced detailed maps.

The botanical results of the expedition appeared as the fifth volume of the expedition reports in 1889, after a number of preliminary papers. The collections of Savatier made in 1877-79 were treated in this connection. The flowering plants and ferns were described by Hariot (1884), with general comments on the

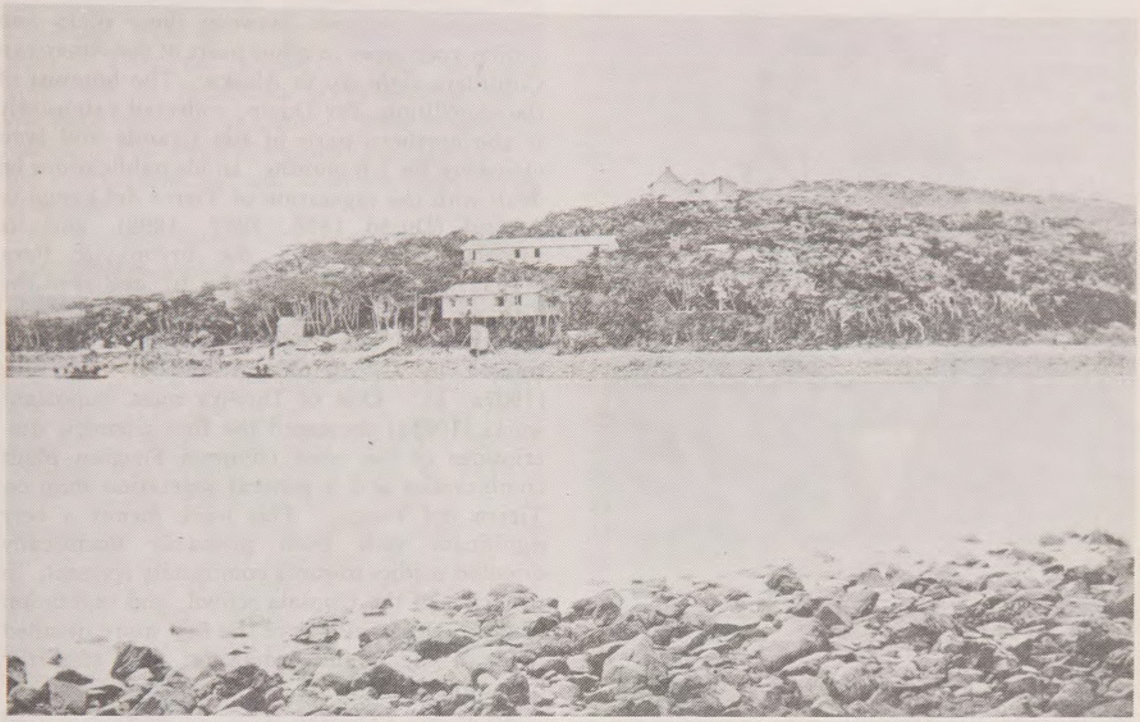

Fig. 38. The French research station of the "Mission Scientifique de Cap Horn" erected at Bahía Orange on Peninsula Hardy, Isla Hoste, in 1882-83. Martial (1883).

flora and vegetation, and Franchet (1889), mosses by C. Müller (1885) and Bescherelle (1889), hepatics by Bescherelle & Massalongo (1889), lichens by Hariot (1887) and Müller Argoviensis (1889b), and algae by Hariot (1889). In all groups new species were described.

The fourth volume of the expedition reports, published in 1887, contained new geological results. The greater part of the rock-specimens described by Hyades (1887) derived from the west and south coast of Isla Hoste, but also rocks from other parts of the southern archipelago were treated. It was up to that time the best and most detailed description about the geology of the region.

In 1890-91 the Frenchmen H. Rousson and P. Willems made significant collections on the Atlantic coast and the northern interior of Isla Grande and on Isla Dawson. In addition to botanical collecting, they made brief observations on geography, climate, fauna, mineralogy, etc., and on the natives, in particular (Rousson & Willems 1891). From their collections Hariot (1900) listed 118 flowering plants, 24 of which were new records for Tierra del Fuego. Hariot (1891) also listed mosses, hepatics, lichens, algae and fungi, some of which were new species for science or new for the region.

5. The emergence of vegetational and ecological studies. Epoch of great monographs (1890-1930)

Towards the end of the last century there were three major research endeavours in Tierra del Fuego. The Russian botanist Nicolas Alboff, emigrated to Argentina, spent two months in 1896 in the region of the Beagle Channel. He made extensive collections comprising 350

Fig. 39. Otto Nordenskjöld (1869-1928), a Swedish geologist and explorer. Nordenskjöld (1898a).

different species, e.g. the first notable collection of the Fuegian high mountain flora (Alboff 1902, a posthumous work Alboff & Kurtz 1896). He did much to develop the herbarium of Museo de La Plata (Moore 1983a: 7). Alboff (1896) also gave a description of the vegetation, regions and formations in Tierra del Fuego, taking the altitudinal differentiation into consideration as well.

In addition to Alboff, Tierra del Fuego saw, two ambitious expeditions during the last decade of the nineteenth century, one from Sweden, and the other from Belgium. The Swedish expedition "Swedish Expedition to the Magellan Territories" was led by the famous geologist Otto Nordenskjöld (Fig. 39) in 1895-97 (Nordenskjöld 1898a, b). His contributions (e.g. 1897a, b, 1898c, d, 1899, 1901, 1907) on the geology and geomorphology of Tierra del Fuego are highly recognized. He was the first to publish a geological map (1899) of Tierra del Fuego and southern Patagonia. One of the most important results of his investigations was the detailed description of the so called Andean diorites, the big granitic and dioritic rock-complexes of the outer Pacific sector. He pointed out the petrological relation between these rocks and similar rock types in other parts of the American Cordillera right up to Alaska. The botanist of the expedition, Per Dusén, collected extensively in the northern parts of Isla Grande and even elsewhere for 5-6 months. In his publications he dealt with the vegetation of Tierra del Fuego in general (Dusén 1896, 1897, 1898), and its vascular flora (1900), the bryophytic flora (1903b, c, 1905a, b, c, 1906a, b), and even the Tertiary flora (1907a). Hepatics were studied by F. Stephani (1900, 1901). Fossil collections were treated by G. Steinmann and O. Wilckens (1907a, b). One of Dusén's most important works (1903a) presented the first scientific descriptions of the most common Fuegian plant communities and a general vegetation map on Tierra del Fuego. This work meant a very significant shift from primarily floristically oriented studies towards community research, in the spirit of the Uppsala school, and vegetation studies. Dusén also gave the first more detailed notes of the inland vegetation, just after the beginning of the boom of sheep husbandry.

All in all, this Magellanic expedition started the frequent visits of Nordic researchers to Tierra del Fuego. It is probably no exaggeration to state that this Swedish expedition as well as the two subsequent ones at the beginning of our century raised many branches of scientific research to a new, modern, level.

The Belgian Antarctic Expedition, led by Henryk Arctowski, spent some time in Tierra del Fuego in the summer of 1897-98, and the botanist of the expedition, M.E. Racovitza, was able to collect plants in parts of the western and southeastern archipelago (Arctowski 1901). His collections were not, however, particularly significant. They were studied by de Wildeman (1905), who also gathered together earlier records. But the most interesting aspect in his studies was the so far first "island biogeographic" attempt to compare the size of the floras of certain islands of the Fuegian archipelago. He showed, for instance, that the flora of Isla Grande contains four times as many species as that of Staaten Island. All in all, he listed about 90% of the vascular plant species currently known to be Fuegian.

As showed by the listing of de Wildeman (1905), by the beginning of this century the floristic data were almost complete especially with regard to the vascular plants, and Princeton University published the first flora of Patagonia (Macloskie 1903-06, 1907, Macloskie et al. 1914). Princeton University had arranged expeditions to Patagonia in 1896-99 covering differente branches of science. They resulted in a monumental series of reports (Hatcher 1903). The expeditions did not, however, visit Tierra del Fuego.

The Swedish Antarctic Expedition in 1901-03 under the leadership of Otto Nordenskjöld was mainly directed to Antarctic islands, but it also made landings in the southern part of Tierra del Fuego (J. Andersson 1902, 1903a, b). The botanist of the expedition, the young Carl Skottsberg (Fig. 40), spent only a rather short period in Fuegia, principally along the Beagle Channel. However, he was able to publish several studies, especially on ecology of many Fuegian species (Skottsberg 1905a, 1906b, 1909) and he also discussed problems related to the phytogeographical positions of Tierra del Fuego (Skottsberg 1904, 1905b). Mosses and lichens were studied by Cardot (1908, 1911) and Darbishire (1912), and hepatics by Stephani (1905).

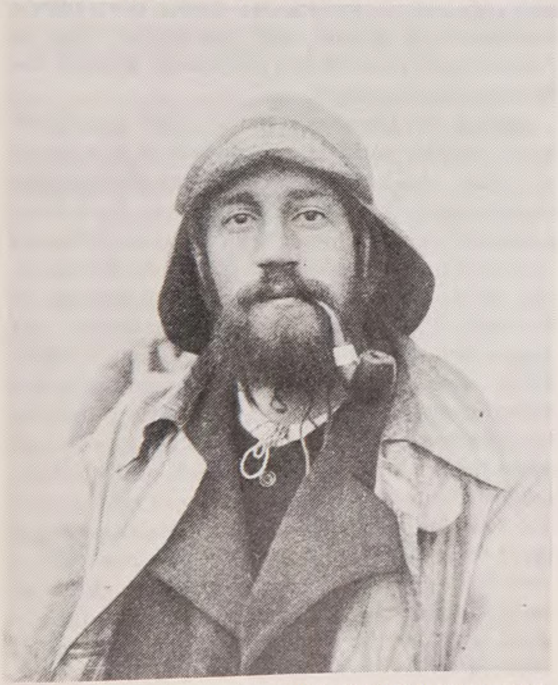

Fig. 40. Maybe the most travelled Swedish botanist, Carl Skottsberg (1880-1963). The photo was probably taken during the second South Polar expedition; Skottsberg (1911).

Cardot treated the whole mossflora of southernmost South America, and that of South Georgia and the Antarctic. He summanrized all the earlier records of more than opne hundred years of exploration. J. Andersson, a geologist, investigated the important fossil-locality of Bahía Tekenika on Isla Hoste, discovered by Dana in 1839, and made also observations on glacial and fluvio-glacial deposits in the Beagle Channel and at Lago Fagnano (J.Anderson 1907). Unfortunately, his fossil collections and Skottsberg's plant collections were largely lost when their ship, the Antartic, was wrecked in February 1903 (J.Andersson 1907).

The experiences from the Antarctic Expedition stimulated Skottsberg to revisit the area in 1907-09 during the Swedish Expedition to Patagonia and Tierra del Fuego under his leadership (see Skottsber 1908-09a, b, 1911). The expedition moved southwards along the Andes from Bariloche to Tierra del Fuego and visited also the Falkland Islands.

Skottsberg collected extensively, expanded his ecological studies and described a great number of plant communities (1910, contains a coloured vegetation map of Tierra del Fuego and Patagonia; 1916, 1921, 1931; see also Anonymus 1963). Especially the monumental publication of 1916 is fundamental to all subsequent studies of the Fuegian vegetation and flora. When examining the botanical results of the Swedish expeditions of 1901-03 and 1907-09, Turril (1919) mentioned that the division of Fuegia and Patagonia into clear botanical provinces and zones is a noteworthly addition to geographical botany. The hepatics, lichens and mosses of the Skottsberg collection were studied by Stephani (1911), Zahlbruckner (1917)and Cardot & Brotherus (1923), respectively.

The geologist of the Skottsberg expedition, P. Quensel, mainly investigated the younger vulcanism of the Cordillera and prepared a geological map of southern Patagonia and Tierra de Fuego (Quensil 1910b). The paleontologist G.T. Halle was able to continue Andersson's research on plant fossils at Bahía Tekenika (Halle 1913). He (1910) also made observations on Quaternary deposits and changes of sea level.

Resource management and assessment aspects attained more emphasis after the foundation of the first estancia in Tierra del Fuego, Estancia Harberton by the Beagle Channel in 1886 (T. Bridges 1892, Martinić 1973, Goodall 1979), which meant the beginning of pastoral development with all its consequences in Tierra del Fuego (Moore & Goodall 1977).

At first the utilization of the windy Fuegian landscape was an enterprise of pioneers. However, quite soon the Chilean and Argentine governments began to assess the resources of their southermost territories. The logging potential of Isla Grande was studied by E. Holmberg (1906) and M. Rothkugel (1916), the value of the Fuegian mires by G. Bonarelli (1917, includes a good summarizing description of the physical geographical conditions in Tierra del Fuego with a geologic map, vegetation map, mire- type map and precipitation map, and a relatively comprehensive bibliography), and J.R. Guiñazu (1934) a little later. Descriptive narratives were provided by Popper (1887), T. Bridges (1892, 1893), Tello (1896), Dabbene (1904), de Agostini (1924) and Plüschow (1930), among others.

A few other Argentine and Chilean botanists visited Tierra del Fuego during the first decades of our century (e.g. Dabbene 1904, Autran 1905), but, in general, they did not add significantly to the knowledge of the Fuegian flora and vegetation. One remarkable exception was Carlos Spegazzini (1924), having visited Tierra del Fuego 41 years earlier, now made comments on the invasión of alien flora and changes in natural vegetation and flora, which were marked.

Similarly, in the fields of geology and geomorphology very few advances were made except those by the three Swedish expeditions mentioned above. However, this situation changed in the middle and at the end of 1920's. The Swedish geologist Carl Caldenius, employed by the Argentine government, made thorough investigations in the 1920's in Fuego Patagonia (see Caldenius 1931). In 1932a he published a classic work on the Quaternary glaciations in Patagonia and Tierra del Fuego. He made an attempt to coordinate the moraine systems connected to the Patagonian Andes with the north European ones, and accordingly, paralleled the glaciations in the Northern and the Southern Hemispheres.

6. The Auer expeditions (1928-1952)

The first Finnish expedition to Tierra del Fuego in 1928-29 sent by the Geographical Society of Finland was of very great scientific importance. It was led by the versatile researcher, geographer, geologist, palaeontologist Väinö Auer (see Auer 1929, 1933b, 1934, Kranck 1930a, b, Gunkel 1942, Tuhkanen 1988, Alhonen 1989, Tuhkanen & Niemelä 1989). This was followed by a number of other expeditions (totally 14) under the leadership of Auer (e.g. Auer 1954, 1958b, 1936c, 1964, 1972, Alhonen 1989). They remained mostly on the Patagonian side, but in 1937-38, 1947-48, 1950 and the last time in 1952 they were extended to Tierra del Fuego.

However, the first expeditions is of most legendary fame and many of the very fundamental ideas were discovered during it. In addition to Väinö Auer, the members of this expedition were the geologist E. Hakan Kranck, the botanist Heikki Roivainen, and a student of geology, Esa Hyyppä as assistant (Fig. 41). In the 1940's and 1950's a number of Argentine researchers participated in the Auer expeditions.

The majority of Auer's expeditions were multidiciplinary and , accordingly, the spectrum of research problems was wide, from petrology of rocks to the taxonomy of certain plant genera. The original incentive for these expeditions was to compare conditions and phenomena connected to glacial and postglacial time in Norden with more or less equivalent areas in the Southern Hemisphere.

During the decades since the first expedition many notable publications appeared as a result of the work of the Fuego-Patagonian expeditions. The majority of them have been gathered together into eleven volumes ("Results of the Finnish Expedition to Tierra del Fuego" I-III, published by the Geographical Society of Finland; "Wissenschaftliche Ergebnisse der Finnischen Expedition nach Patagonien 1937-1938 und der Finnisch-Argentinischen Expeditionen 1947-53, 1957" I-VIII, published by Academia Scientiarum Fennica). Shortly after the first expedition Kranck published his extensive work on the geology and tectonics of the sourthern part of the Andes with a geological map of Tierra del Fuego (Kranck 1932). Another large book, "Verschiebungen der Wald- und Steppengebiete Feuerlands in postglazialer Zeit" by Auer, appeared in 1933. It examined the shifts between steppe and forest in the postglacial time. The work included numerous bog profiles with pollen diagrams and isochrone maps showing the location of the boundary

Fig. 41. The expedition team of the Geographical Society of Finland 1928-29. All of them were young, 26-33 years of age at the time of the expedition, now they have all departed this life, the last one, Prof. E.H.Kranck, died in Canada in September 1989. Photo from Auer (1929:19).

between steppe and forest at different times.

Perhaps the most central result of the Auer expeditions was the discovery and development of applications of tephrachronology in the study of the Quaternay history of Tierra del Fuego (Auer 1941, 1950, 1958a, 1959, 1960, 1963a, b, 1965, 1970, 1974). In the beginning the tephrachronology was naturally only relative, but absolute datings became possible in the 1940's. Auer applied tephrachronology in a simplistic way, and it has been shown that he made lots of misinterpretations (e.g. Rabassa 1987, Stern 1990). One of the most fatal errors Auer committed was to reject an important radiocaron dating from "La Misión" profile made from a bog near Río Grande which did not support his sea level chronology (Auer 1974, cf. Markgraf 1980a, b, 1983).

According to Auer, the struggle between forest and steppe reflecting variations in climate have been the same in Tierra del Fuego and southern Patagonia as in the Northern Hemisphere. He concluded that climatic fluctuations have been contemporary in the earth, which means that also glaciations have been contemporary in the Northern and southern Hemisphere. In principle, this seems to be a correct generalization even in the light of the newest research results (cf. Rabassa 1987, Heusser 1989, Clapperton 1990, Rabassa et al. 1990).

In connection with the retreat of the forest border, Auer introduced the concept of "The Desert Devil" (Der Demon der Wüste; i.e. a relative to Der Polardemon, the Polar Devil, discussed in the high North; Auer 1935, 1939), referring to the general regressive tendency of forests and the expansion of steppes and, behind these, deserts. The newest evidence does not, however, support this suggestion (e.g. Veblen & Lorenz 1988, Veblen & Markgraf 1988). On the other hand, it is clear that the pastoral development and overgrazing has expanded steppes, and Auer has already paid attention to this phenomenon (Auer 1951a, b; E. Kalela 1941c, d, 1949).

Gradually Auer created hipotheses on great connections between sea level transgressions and volcanic eruptions on the one hand, and between these transgresions and advancements of forest border on the other. The "La Mision Profile" (first drawn in 1952, for the latest version, see Auer 1974) was in a sense a synthesis of his life work, a kind of global watch where synchronic phenomena were paralleled by the changes in sea level.

After the 1928-29 expedition Hikki Roivainen published several floristic notes from southern Chile (Roivainen 1933a, b, 1934, 1936). Studies of the extensive moss collections were published later (Roivainen 1954b, 1955), partly in cooperation with E. Bartram (Roivainen & Bartram 1937), and partly the results were presented by other bryologists (Bartram 1946, Engel 1976, 1978). Still, however, a large part of the collections remain unstudied. In his ecological and phytosociological work Roivainen concentrated on mire vegetation. In his studies he applied the Cajanderian forest and mire type concept which considers the leading role of site factors and combines all seral vegetation. He also made some ecological measurements. His main work was published after several delays in 1954 (a), and it reflects in many respects modern ideas of vegetation studies. Roivainen returned to Tierra del Fuego in 1969-70 in order to complete his collections, and his last paper on South American bryophytes was published two years later (Roivainen 1972).

Veli Räsänen (1932), who did not himself participate in the Auer expeditions, published a study of the lichen specimens collected by Roivainen. Th. Sahlstein (1933) prepared a study of chemical-petrological composition of tephra layers.

Erkki and Aarno Kalela, who participated in the Auer expedition to southern Patagonia in 1937-38, worked only on the Patagonian side. They tried to implement their father's (A.K. Cajander) forestry and vegetation theories into foreign, distant conditions. Erkki Kalela was a forester, who studied the distribution, succession and growth of various Patagonian trees in different sites (E. Kalela 1941 a, b, c). At the same time he gave the first silvicultural basis for the future management of the Patagonian forests. Aarno Kalela was both taxonomist and vegetation scientist. He concentrated on the floristic composition of these Patagonian forests (E. Kalela 1940) and tried to define an analogous site type system (1941) in austral forest vegetation as was in use for Finland. However, all the numerous Patagonian relevées made by A. Kalela remain unpublished. Only some preliminary groupings of Patagonian vegetation and essays on general phytogeography have been prepared (A. Kalela 1946, Pyykkö 1966) and a rough scheme of the site type system for southern Patagonia (A. Kalela, 1941).

Taken all together, the research done by Auer and his expeditions has been of great historical significance for both Finnish and Argentine scientific research. In some cases the conclusions drawn by Auer have emerged rather as a consequence of his impulsive character than cool judgement and analysis. The results have gained reputation all over the world. His works have received much recognition, although there is no lack of objection, and indeed, in many cases even very basic revision is needed. But what is most important, is that Auer created a strong base for continued investigations and raised questions which still lack answers or verifications and which cannot be ignored.

7. Up to our days: the tradition of expeditions continues (1960)

An increasing number of individual botanists and other natural scientists or expeditions visited Tierra del Fuego as communications improved. But relatively few really noteworthy scientific advances were made in Tierra del Fuego during the period after the Finnish expedition in 1928-29 up to the early 1960's. In the field of botany, one of the exceptions is perhaps Ruiz-Leal (1954), who paid attention to the increasing number of alien flora along the north shore of the Beagle Channel.

The Royal Society, London, arranged an expedition to southern Chile in 1958-59 (Holdgate 1960, Godley 1963) in order to obtain more information on the biogeography of the higher latitudes of the Sourthern Hemisphere by making biological and geological observations at stations between 42° and 56° S. The main studies were focused on Chiloé, Wellington and Navarino. The expedition made an attempt to gather as complete a collection of herbarium specimens as possible.

The leader of the research team of the Royal Society Expedition, M.W. Holdgate, gave one of the first precise descriptions of Fuegian soils on Isla Navarino (Holdgate 1961a). A few years earlier, Milano & Marzocca (1954) had described a couple of soil profiles from Tierra del Fuego. Diaz et al. (1959-60) published their soil studies from the regions which are of most significance for agriculture in the Magallanic area. Pedological studies were continued by Etchevehere (1972). Pisano (1977a) provided a synthetic description of the Fuegian soils and their connections with vegetation. The most substancial contribution is, however, provided by Frederiksen (1988: with a map of the distribution of soil types). The study is based on field work and satellite imaginary interpretations.

Frederiksen was a member of the Danish multidiciplinary expedition in 1978-79 (Madsen et al. 1980), which continued the Nordic research tradition in the area since the last Auer expedition to Tierra del Fuego in 1952. During this expedition most of the field work was carried out in the Patagonian side. The expedition comprised geographical, botanical and zoological projects. In Tierra del Fuego the research topics were soil development in relation to climate, entomology of Lepidoptera, collectiong of *Nothofagus* seed for forestry experiments in the Faeroe Islands and studies of snowbed vegetation and alpine life-forms. The preliminary results from the transplantations on the Faeroe Islands have been presented by Odum (1985 and Odum et al (1989) (see also Tuhkanen 1987).

A new nation among those which have sent expeditions to Fuego-Patagonia was Japan in the 1960's. The expeditions were geologic-botanical in character (Seki 1974). The first from the Universities of Hokkaido and Hiroshima was realized in 1965 and it focused on Tierra del Fuego, the second in 1967 on more northern regions in Patagonia around Península Taitao as target. The botanical objetives comprised the study of floristic relations between Antarctica and Fuego-Patagonia, and between the Andes and East Asia with main emphasis on moss and lichen floras (see Asahina 1965). These studies were continued by Japanese cryptogamic botanists in 1980's (see Inoue 1984).

Natalie Goodall (see Goodall 1971), the first botanist resident in Tierra del Fuego, since 1964 through her explorations has increased knowledge of distribution and occurence of Fuegian plants, especially in southern and eastern Isla Grande and on Staaten Island and elsewhere (e.g. Goodall 1980, 1981). She has also provided a comprehensive description of the nature and history of Tierra del Fuego with bibliography (Goodall 1979).

The Instituto de la Patagonia in Punta Arenas was founded in 1969. it started an extensive programme studying the ecosystems in the region of Magallanes. As a part or this studies of the vegetation and flora of the Chilean parts of Fuegia have considerably increased our knowledge of the nature of the Magellanic region (Pisano 1970, 1971a, b, 1972a, b, 1973a, b, 1974, 1975, 1977a with a vegetation map in the scale 1:1 mill., 1980, 1981, 1982, 1983a, b, 1985-86, 1987, Pisano & Dimitri 1973; Pisano & Schlatter 1981a, b; Pisano & Venegas 1984; Dollenz 1977, 1978, 1980, 1981, 1982a, b, c). A herbarium was also gathered during this research programme (Dollenz 1974). In addition to wide biological and ecological research, the lines of work of the Instituto comprise also history and social sciences.

An American research vessel, R/V Hero, financed by the National Science Foundation, has cruised much in the Fuegian waters and transported a number of scientists. In the austral spring 1969 she made three cruises through the channels of the southern Chilean archipelago. The first cruise was devoted mainly to cryptogamic and phanerogamic botany, and large collections were made throughout the archipelago (Imshaug 1970, Young 1970). The second was devoted primarily to marine biology (Kaesler 1970). The third supported shorebased geologic and geophysical work (Halpern 1970, 1973). During the three cruises approximately 1.000 collections of vascular plants were made, as well as wood samples for age and growth studies (Young 1972).

The joint United States-Argentina botanical expediton aboard R/V Hero to Staaten Island and the nearby coastline of Península Mitre was undertaken 1971 to study, survey and document with herbarium specimens the flora of these locations (Imshaug 1972, Crow 1975, Dudley 1981, Dudley & Crow 1983 including a comprehensive bibliography). The collections made form the largest and most complete representation of the island'd vascular plant and fern flora. CEBIMA (Centro de Investigación de Biología Marina) carried out biological and oceanographical research on Staaten Island a few years earlier, in 1967, under the leadership of O. Kühnemann (1977). Staaten Island was relatively frequently visited by early voyagers, but it was largely forgotten subsequently until the expeditions mentioned above.

An Italian expedtion (AMF Mares-Gruppo Ricerche Scientifiche e Tecniche Subaque) was sent to Patagonia, Tierra de Fuego and Antarctica in 1973-1974. The main objetives of this expedition, consisting of 28 members, were the study of some specific problems of marine biology, palaeontology, ecology and palaeoecology of the South American continent and Antarctica, and the collection of botanical and zoological specimens from regions of particular biogeograhical interest (Pichi Sermolli & Bizzarri 1978).

One of the most remarkable botanists of our time to be mentioned in this context is David M. Moore, who has concentrated on the flora of Tierra del Fuego. Since the beginning of 1970's his several visits to Tierra del Fuego (and the Falkland Islands) have resulted in a number of publications (Moore 1972, 1974, 1975, 1979, 1981, 1983a, b, c, Moore & Chater 1971; Moore & al. 1972; Moore & Goodall 1977). The flora of Tierra del Fuego (Moore 1983a) with distribution maps is one of the recent mile stones in the history of botanical research of Tierra del Fuego.

Geological knowledge has increased along with economic ambitions, i.e. oil prospecting (e.g. Thomas 1949, ENAP 1978). On the bachground of the theory of plate tectonics the Scotia Arc Tectonic project 1969-1975 in the field work transported by R/V Hero solved many questions on the relationship between the southern South American part of the Andes and the Antarctic Peninsula (Dalziel & Elliot 1973, Dalziel et al. 1974, 1975, Palmer & Dalziel 1973, Dalziel 19875, Dott et al. 1982, Winn & Dott 1978, Winn 1978).

In terms of the International Geological Correlation Programme, a specific project entiled "Quaternary of South America and Antarctic Peninsula" started in 1983, provided a great number of valuable contributions to the Quaternary history and Holocene climatic changes in Tierra del Fuego (e.g. Porter et al. 1984, Rabassa et al. 1986, 1990, Heusser & Rabassa 1987, Heusser 1989a, b, Rabassa & Clapperton 1990), this work still continues.

Museo Territorial de Tierra del Fuego and CADIC (Centro Austral de Investigaciones Científicas), both located in Ushuaia, deserve to be mentioned as important local research centres. Their activity comprises inventories and research both in natural and social sciences, with applied aspects as well (e.g. Bianciotto 1986, Collantes et al. 1985, 1989a, b, c, Bondel 1988).

V. THE RESEARCH PROJECT "THE BIOGEOGRAPHICAL POSITION OF TIERRA DEL FUEGO IN RELATION TO OTHER ANTIBOREAL AND BOREAL REGIONS"

The research project here presented is named *"The phytogeographical position of Tierra del Fuego in relation to other antiboreal and boreal regions"*, and an entomological project connected to this is entitled *"The occurence of Carabid beetles (Coleoptera; Carabidae) in Tierra del Fuego"*.

Two members of the present research team, Ilpo Kuokka and Sakari Tuhkanen, visited Tierra del Fuego for the first time in 1984-85. During a period of a few weeks they carried out preliminary field work, collected vascular plants and made contacts with local research institutions in Ushuaia and Punta Arenas. The second expedition was undertaken in 1986-87, the whole present team participating see (Fig. 42).

The objetives this project can be summarized as follows:

— to study the regional variation in vegetation in relation to important ecological gradients, i.e. to describe and classify Fuegian plant communities.
— to supplement the knowledge about the distribution and ecology of plant and insect species; connected to this also a great number of plant and insect specimens were collected.
— to determine the areas which in an ecoclimatic sense correspond to Tierra del Fuego, and in terms of these areas define plant and insect communities (vicariates) which ecologically correspond to each other in Tierra del Fuego and in the Northern Hemisphere.

A very central aspect is the comparison of both hemispheres, to compare Tierra del Fuego with ecoclimatically equivalent areas in oher parts of the world.

The ideological background of this project is, in a sense, based in the Finnish climatic-phytogeographical school" (see Ahti & al. 1968, Hämet-Ahti & al. 1974, Hämet-Ahti 1981, 1986 with vegetational emphasis, and Tuhkanen 1980, 1984, 1986, 1987 for climatic emphasis), which in turn is based on a long tradition in

Fig. 42. Our team in good spirits at camp fire in the eastern part of the main island in Península Mitre, in a *Nothofagus* forest in February 1987. The persons from left to right: Sakari Tuhkanen, geographer, Soili Stenroos, lichenologist, Jaakko Hyvönen, briologist, Jari Niemelä, entomologist, and Ilpo Kuokka, botanist. Photo: Sakari Tuhkanen (1987).

Fig. 43. In the field works of the present project numerous vegetation relevée analyses were made. In the picture two researchers investigating a relevée near San Sebastián, west of the Bahía, in a scrub steppe area. Photo: Jari Niemelä (1986).

Finnish-botany (J.P. Norrlin, A.K. Cajander, Kaarlo Linkola, Viljo Kujala, Aarno Kalela) with contacts the thinking of such scholar's as August Grisebach, Eug. Warming and A.F.W. Schimper.

The project is connected whith the long Nordic research tradition in Tierra del Fuego (Daniel Solander, Otto Nordenskjöld, Per Dusén Carl Skottsberg, Carl Caldenius, Väinö Auer, E. Hakan Kranck, Heikki Roivainen, to mention some of the most notable names). In addition, taxonomic studies of cryptogams of Tierra del Fuego have been undertaken since the last century by Nordic scientists (William Nylander, Per Dusén, E.A. Vainio, V.F. Brotherus, Veli Räsänen, Rolf Santesson). In the field of zoology there are very weak traditions in research at Tierra del Fuego, especially as far as the terrestrial fauna is concerned, many of the previous works being inventory in character. In this sense the faunistic-ecological carabid-project is of a pioneering nature. Our project is more biogeographically and biologically orientated than were the earlier Finnish expeditions to Tierra del Fuego and Southern Patagonia, led by Väinö Auer.

The practical aim of our fieldworks is to obtain a comprehensive, systematically gathered phytosociological-ecological material, which could constitute a base for different treatments. During the fielwork a number of relevées (ca. 80) were analyzed, which as a rule, were 400 m² in size (Fig. 43). We made attempts to gather as representative a collection of relevées of vegetation in (relatively seen) mesic sites as possible from different parts of Tierra del Fuego. An analysis of the structure and floristic composition of vegetation was completed by certain observations on soils. The insect fauna within the same relevées was also investigated.

Our itinerary in Tierra del Fuego and southermost Patagonia in 1984-1985 (IK & ST) and 1986-87 (the whole team) covered many parts of the central and eastern Isla Grande and the vicinity of Punta Arenas (Fig. 44). We also made visits to Isla Clarence and Isla Furia, and to Isla Navarino. The routes were traveled by foot or by using cars, horses, boats, aircraft or

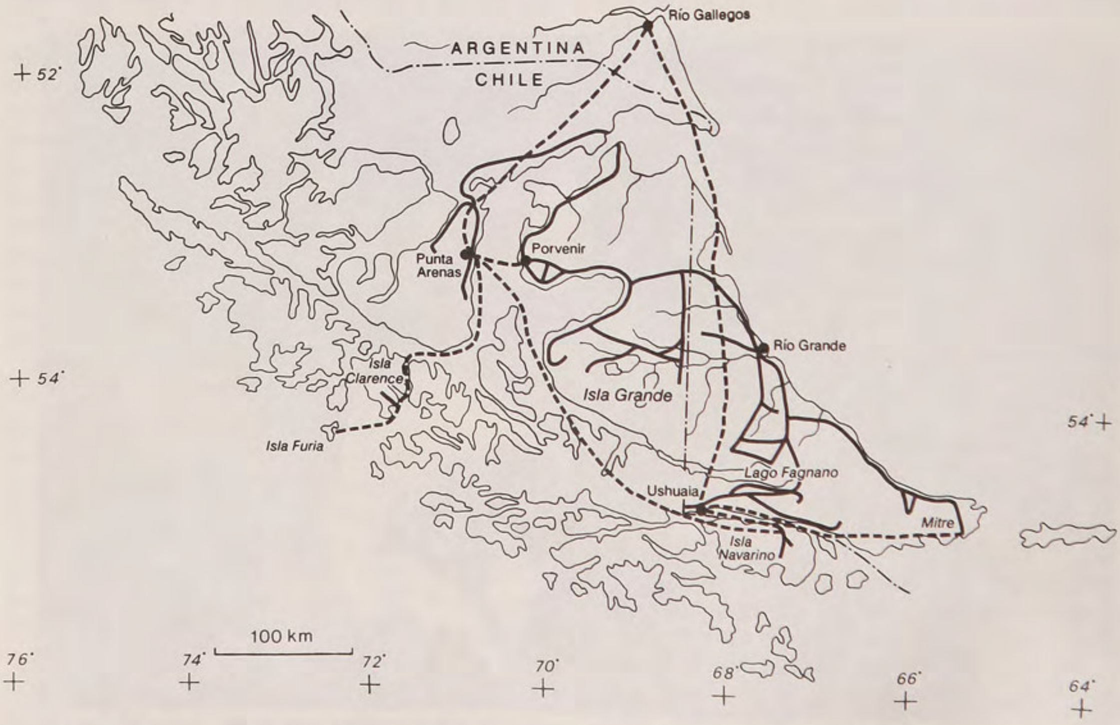

Fig. 44. The itinerary in Tierra del Fuego and parts of southern Patagonia covered by the present project in 1984-85 (IK & ST) and 1986 – 87 (the whole team) helicopter (broken line).

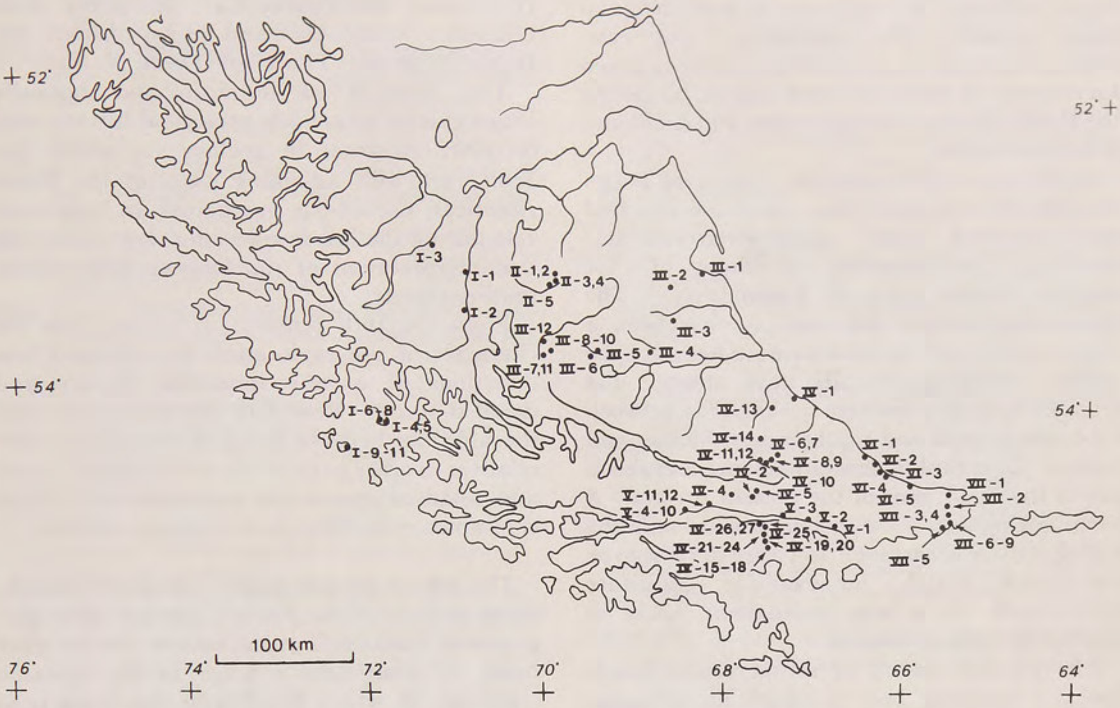

Fig. 45. Locations of the relevées analyzed in 1986-87. The localities form seven transects (I-VII), in which both the horizontal and vertical transitions in climate are reflected.

helicopters.

Our expedition has been described by Tuhkanen et al.(1986), Paalanen (1987), Tuhkanen (1988, 1990b) and Tuhkanen & Niemelä (1989). Some preliminary reports were published in Argentina (Kuokka 1989, Tuhkanen 1989, 1990a). The main entomological, phytosociological and ecoclimatical results are treated by Niemelä (1990), Kuokka (1990) and Tuhkanen (1990), respectively. Taxonomic studies of the lichen flora are included in Stenroos (1987, 1989a, b), Ahti et al. (1990), Stenroos & Ahti (1990) and Stenroos et al. (1990). Mosses are dealt by Hyvönen (1991a, b). Hevy metal compositon in *Sphagnum* specimens is also studied (Mäkinen et al. in Press).

The specimens collected are deposited at the Botanical Museum of the University of Helsinki (H) and duplicates of the hepatic specimens in Jena (JE). The localities form seven transects, in which both the horizontal and vertical transitions in climate are reflected (Fig. 45).

VI. DISCUSSION AND SUMMARY

The present paper makes an attempt to outline the main physical geographical conditions in Tierra del Fuego with an extensive series of maps and the principal gradients in the Fuegian vegetation and to examine the history of scientific research in Tierra del Fuego with special reference to phytogeographical and botanical research. It gives a physical geographical and historical background for the Finnish project in biogeographical research presented in this works and at the same time some bibliographical value is conferred on the paper by references to the majority of geographical, geological and botanical publications on Tierra del Fuego.

The backbone and the most decisive physical geographical factor in Tierra del Fuego is the Andean Cordillera system which bends eastwards before submerging into the Scotia Arc sea. It bring about abrupt changes in topography and climate in short distances and gives a pronounced dualistic character to Tierra del Fuego, which is clearly reflected in vegetation as a sequence of plant formations from southwest to northeast, from open moorlands and scrubs with evergreen rainforestes in more sheltered places, bordering the Pacific Ocean, through mixed and deciduous forests to steppes.

In the Southern Hemisphere, Tierra del Fuego is almost the only land area, where one can find environmental and palaeoenvironmental conditions corresponding to those of, for instance certain parts of Scandinavia. The Quaternary history, for example, has been a target for intensive comparative studies since the 1920's. Biogeographically little attempt has been made to demonstrate parallelisms between the northernmost and southernmost biomes and regions. By means of ecoclimatic methods this is one of the main aims of the present project. A complicating factor in this context is that the highly oceanic areas, such as Tierra del Fuego or the Faeroe Islands, for example, constitute problematic, in a way anomalous, areas in phytogeographical systems.

The natural history of southernmost South America has long been a target for intensive scientific investigation. Since the days of Charles Darwin and Joseph Dalton Hooker a series of expeditions and individual researchers have worked in the area and produced a voluminous literature. Because of the relatively easy access, much of this work was concentrated on the pampas and deciduous forests. Data has accumulated, but many problems remain. There are still unknown parts in Tierra del Fuego, although without doubt it is one of the best known areas in the entire South America from the botanical, geographical and geological points of view. This is due to its interest from a scientific aspect as well as to its geographical location, an obligatory route for circum-navigations of the world in early eras.

Some of the most important cornerstones in the research of Tierra del Fuego have been the first and second Cook circum-navigations with Joseph Banks, Daniel Solander and J.R. & J.G. Forster on board, then Charles Darwin, Joseph D. Hooker, Per Dusén, Carl Skottsberg, Carl Caldenius, Väinö Auer and his expeditions, Ian Dalziel, Edmundo Pisano and David M. Moore.

The basis is of floreistic and faunistic biogeography rests upon geological history, and therefore advances in geology -in which the Scotia arc with adjoining parts of the South American Cordilleras has played an important role during the last few decades- are crucial for the interpretation of the biogeography of the southern lands.

From the 16th century up to our days the character of the exploration has changed into directions of a more scientific inquiry and detailed study. Researchs are concerned with the affinities between Fuegian plants and their relatives in other parts of the world, the structure and relationships of the vegetation and plant communities and the human impact on them.

The present Finnish project comprises the apllication of ideas of the Finnish "climatic-phytogeographical" school on Fuegian nature. On the other hand, it constitutes a stage in the research tradition, in which the Nordic emphasis is so obvious, started by the Swedes Per Dusén and Carl Skottsberg almost a century ago. We try to define the variations within Tierra del Fuego itself in relation to the principal climatic gradients and how this is reflected in its vegetation. We have augmented vegetation relevée material, which has been relatively limited.

The faunistic ecological project connected to the main one has also a pioneering nature: the majority of the previous zoological work has been more or less inventory in character and, moreover, the method used, i.e. incorporating vegetational relevée analysis with insect data was very seldom applied.

Tierra del Fuego, Fireland, so often described with wistful tones by explorers and writers, is a land of legends where the fires of the Indians have long died but which still attracts the interest of researchers.

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SE TERMINO DE IMPRIMIR
EN EL MES DE JUNIO DE 1992
EN LOS TALLERES GRAFICOS
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