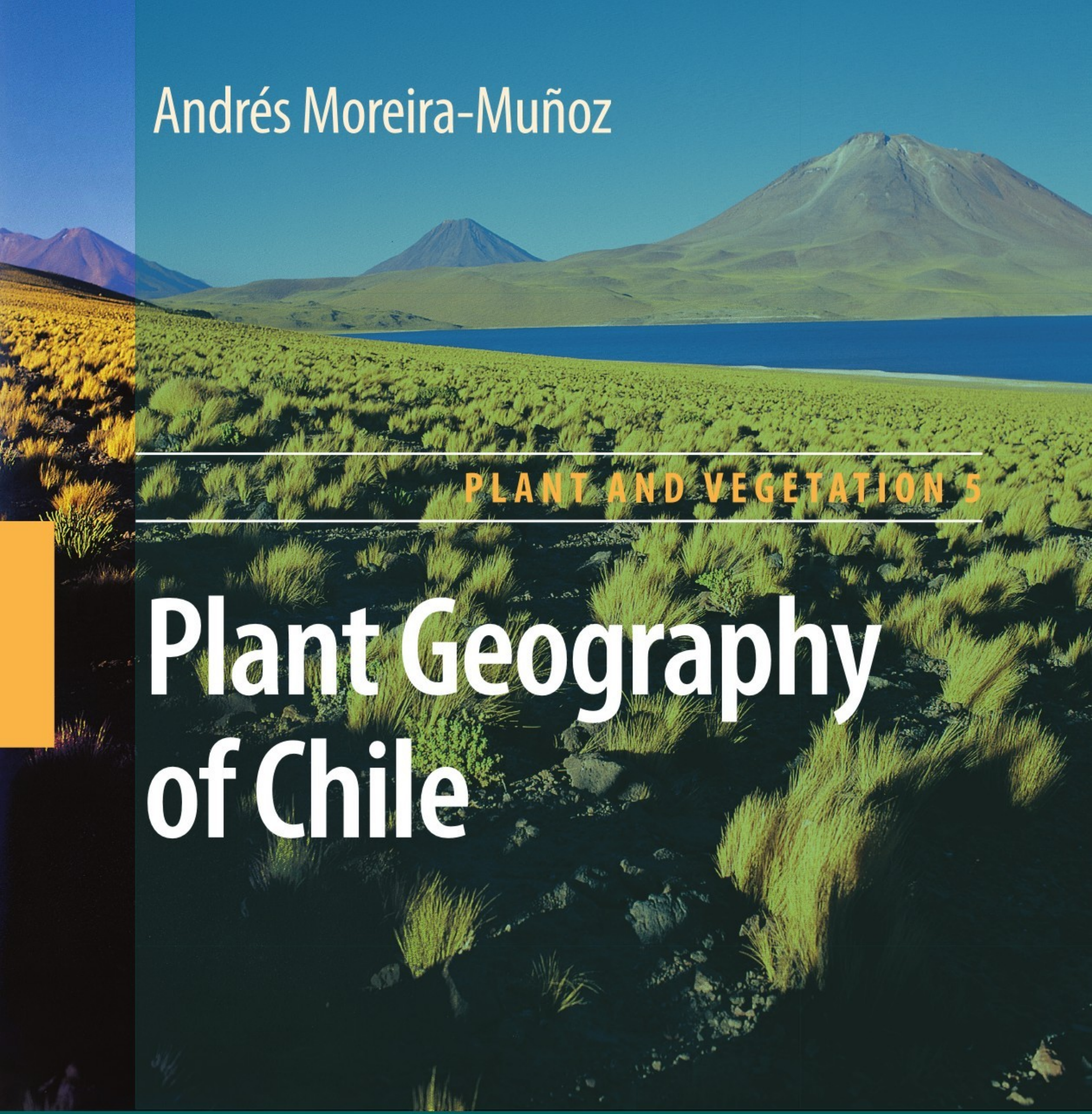

Andrés Moreira-Muñoz

PLANT AND VEGETATION 5

Plant Geography of Chile

Springer

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PLANT AND VEGETATION

Volume 5

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by

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Springer

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Cover illustration: High-Andean vegetation at Laguna Miscanti (23°43′S, 67°47′W, 4350 m asl)

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Carlos Reiche (1860–1929)
In Memoriam

Foreword

It is not just the brilliant and dramatic scenery that makes Chile such an attractive part of the world. No, that country has so very much more! And certainly it has a rich and beautiful flora. Chile's plant world is strongly diversified and shows interesting geographical and evolutionary patterns. This is due to several factors: The geographical position of the country on the edge of a continental plate and stretching along an extremely long latitudinal gradient from the tropics to the cold, barren rocks of Cape Horn, opposite Antarctica; the strong differences in altitude from sea level to the icy peaks of the Andes; the inclusion of distant islands in the country's territory; the long geological and evolutionary history of the biota; and the mixture of tropical and temperate floras.

The flora and vegetation of Chile already drew the attention of the early adventurers and explorers and as from the eighteenth century attracted naturalists and collectors from Europe. In the nineteenth century famous botanists explored and studied the Chilean plant world, and gradually the flora and plant geographical patterns became subjects of scientific analyses both by European and Chilean scholars. Recently, the development of new scientific techniques have allowed to reveal the remarkable evolutionary pathways in many Chilean plant groups, and have provided clues to the origins of intriguing plant geographical patterns in the southern hemisphere floras. This shall be of interest for botanists, plant geographers, ecologists and evolutionary biologists worldwide.

I was very lucky to get into contact with Dr. Andrés Moreira-Muñoz. He is an enthusiastic and outstanding Chilean plant scientist with historical roots in this subject area. Dr. Moreira-Muñoz here presents a modern and stimulating account of the Plant Geography of Chile that analyses the floristic diversity and endemism of the country. He interprets the origins of the fascinating plant geographical patterns of Chile and explains the evolutionary background of the most important plant groups. I am very pleased to present this book as a volume in the series "Plant and Vegetation" to the international readership.

Utrecht, The Nederlands Marinus J.A. Werger

Preface

One morning in 1897 at the Quinta Normal, Santiago: the Director of the Museo Nacional de Historia Natural, Federico Philippi welcomes the new German botanist responsible for taken the reins of the botanical section, Dr Carl Reiche. He has been committed to maintain the National Herbarium, promoting exchanges, analyzing, increasing and organizing the collections of the Herbarium. He will be also, and this is not a trivial thing, responsible for writing the new *Flora de Chile*; and he has already published the first volume. Chilean botanical knowledge showed at the end of the nineteenth century still many gaps, in spite of the great achievements of Claudio Gay and R.A. Philippi, this latter the father and mentor of the Museum's Director. It took Reiche more than 15 years to systematize, revise and add the necessary information that finally encompassed the six volumes of the *Flora de Chile* (Chap. 2). In the meantime, when Reiche was already well familiarized with the Chilean flora, he got a request for writing a synthetic book about the Chilean plant geography for the series *Die Vegetation der Erde,* edited by the great German botanists Adolf Engler and Oscar Drude. Reiche completed the assignment successfully, and 1907 published *Grundzüge der Pflanzenverbreitung in Chile*, encompassing 222 pages with two maps and several photographs (*Vegetationsbilder*). This was the first (and so far the only) *Plant Geography of Chile*. This great effort, which put the Chilean plant world in a renowned world series, only got a Spanish translation 30 years later, thanks to the engagement of G. Looser, himself a botanist and notable scientific communicator (Chap. 2).

Just as Reiche once did with the previous works of Gay and the Philippi, now it seems to be time for a renewal of Reiche's *Plant Geography*. No few things have changed in a hundred years: plants have been renamed and reclassified; taxonomy and systematics have suffered far-reaching changes; biology, geography, and biogeography have undergone paradigmatic vicissitudes. I underwent the challenge of writing a "New Plant Geography of Chile" as a doctoral student in Erlangen, Germany. In such an exponentially dynamic field, one and a half year after the publication of the thesis many things had to be revised and updated for this book.

Regarding the subject, the reader may ask why to use the old concept of "plant geography" rather than "phytogeography" or "geobotany"? As these terms are often used indistinctly, I decided to use the oldest term "plant geography", honouring the seminal works from A. von Humboldt: *Géographie des plantes*, and A.P. de Candolle's *Géographie Botanique* (Chap. 4). The present book also takes inspiration from Stanley Cain's words in his book *Foundations of Plant Geography*: "This is not a descriptive plant geography, but rather an inquiry into the foundations of the science of plant geography" (Cain 1944, p xi) (Chap. 3).

What Is This Book Not About?

This book is not a traditional geobotanical textbook. It rather attempts to enter into the discussion on the challenges that shape (post)modern biogeography in the twenty-first century. A detailed vegetation description, which is sometimes misunderstood as a main task of "plant geography", is very far from the goal of the book. The reader is redirected to recent advances in this specific field (Chap. 1). Many new concepts and methods are currently emerging in biogeography. This book doesn't offer new conceptual or methodological advances; it rather wants to be a "field guide" to the possibilities for the development of the discipline in Chile. Consequently, several conflicting approaches that have been proposed for explaining current biogeographic patterns are confronted throughout the text (e.g. vicariance versus dispersal). The result is mostly not definitive, suggesting that a dichotomy is just a too simple problem design of a much more complex problem.

What Is This Book Then About?

The present book intends to reflect the "state of the art" or a synthesis of the plant geographical discipline in Chile. The challenge is seemingly overwhelming, since in such a composite discipline like biogeography, today any intend to integrate the different views that shape it, must confront the differences inherent to the diverse approaches involved in the discipline. To what extent biogeography assumes and reflects the conflicts, assumptions and challenges inherent to (post)modern science must then be kept in mind while analysing the Chilean plant geography.

This approach leaves us the theoretical basis and practical lines of direction for the endeavour of doing plant geography in the twenty-first century, in the constantly "changing world" of biogeography (sensu Ebach and Tangney 2007) (Chap. 10). Most efforts at the regional level concentrate rather on the descriptive or on the analytical. I would like to do both and also to present the few results in a more general interpretative framework. I would like to accept the challenge posted by Morrone (2009) (Chap. 10), touching methodological as well as more theoretical aspects that will help the student build an own "road map" towards a future development of the discipline in Chile, integrating methods, data, concepts, and interpretations from different fields.

Applying one of the basic principles of geography, for a better comprehension of the subject I have often put the eye beyond the Pacific and beyond the Andes, touching aspects of the New Zealand biota, the Antarctic palaeobiomes, Argentinian Patagonia… I apologize if I have mentioned these aspects in a superficial form.

Nevertheless, I suspect that several aspects of the book are applicable or of interest for biogeographers in the other (once united) southern hemisphere territories; if so, I will be deeply satisfied.

Structure of the Book

The book is divided in five parts that organize the different chapters.

The 1st part presents an overview of the geographical and botanical scenarios that shape the Chilean vascular plant world, in the present as well as in the geologic past. In chapter one, the main physical characteristics of the Chilean territory are briefly exposed, especially the geological and tectonic origins of Chile and their effects on the palaeogeography and the evolution of the Southern Cone biomes. This contributes to a better understanding of the current climate and vegetation. The 2nd chapter makes a succinct revision of the historical development of Chilean botany, and synthesizes the current knowledge regarding the composition of the flora.

The 2nd part deals with Chilean plant geographical relationships, oriented to a synthesis of the floristic elements of the extant flora. The classification of Chilean genera into floristic elements in Chap. 3, will be the basis for the discussion of the disjunct patterns that shape the Chilean flora. This analysis will be further complemented with the task undertaken in the 4th chapter, regarding the biogeographical regionalization of the Chilean territory.

The 3rd part provides an analysis of two close related subdisciplines: island biogeography and conservation biogeography. Chapter 5 presents a synthesis of the plant world of the Chilean Pacific offshore islands, emphasizing their uniqueness and threats, while the 6th chapter analyses the fragmentation in the mainland, related to the impacts of human activities on the Chilean ecosystems. Concepts and tools developed within the field of conservation biogeography are analyzed in relation to current global changes.

The 4th part moves into the case studies, regarding specific groups that deserve special attention in biogeography. Chapter 7 gets into the biogeography of one of the most charismatic American families, the Cactaceae, of course regarding its Chilean representatives. Chapter 8 turns to another not less interesting family, the Asteraceae, the most genus/species-rich family in Chile. The last case study is presented in Chap. 9, devoted to a monogeneric family also called the "key genus in plant geography": *Nothofagus*.

The 5th and last part of the book announces several ways in which Chilean plant geography can further develop; maybe more rapidly and effectively than during the last 100 years? Chapter 10 is in this sense rather speculative, in an attempt to put Chilean plant geography in a more general context of modern biogeography. Finally, the 11th chapter only adds several digressions about the scientific endeavour and the artificial distinction between nature and culture.

Santiago, Chile Andrés Moreira-Muñoz

Acknowledgments

The book was initially developed as a doctoral study at the Geographical Institute of Erlangen-Nürnberg University, Germany. Support in form of a grant was fortunately provided by the German Academic Exchange Service (DAAD). I am much indebted to Prof. Dr. Michael Richter, who was from the first moment the main supporter of the idea. He and his family, together with all the colleagues and workers at the Geographical Institute in Erlangen made our family's stay in Germany a great life experience. From the Geography to the Botanical Garden in Erlangen there are just several blocks, and the support and friendship we found there in the person of Dr. Walter Welss and his family was also a foothold in our stay. Prof. Dr.Werner Nezadal (Erlangen) and Prof. Dr. Tod Stuessy (Vienna) gently assumed the revision of the thesis.

The thesis was improved by the attendance of several conferences thanks to grants from the Zantner-Busch Stiftung (Erlangen). At the conference "Palaeogeography and Palaeobiogeography: Biodiversity in Space and Time", NIEeS, Cambridge, UK, 10th–11th April, I attended the workshop for using the program TimeTrek for plate tectonic reconstructions. I also could attend the XVII International Botanical Congress in Vienna, 17th–23rd July 2005.

The idea of transforming the thesis into a book found absolute support in the person of Prof. Dr. Marinus Werger. He acted not just as a language editor but as a very patient reviewer guiding the editing process in all its stages. The early intention was also promoted by Dr. Leslie R. Landrum and Dr. Juan J. Morrone.

Crucial for the positive development of the book has been Springer's production and editing team: first Inga Wilde and Ria Kanters, and lately Ineke Ravesloot and Annet Shankary. Several colleagues and friends graciously read and commented on draft chapters: Federico Luebert (Berlin), Hermann Manríquez (Santiago), Patrick Griffith (Florida), Malte Ebach (Arizona), Michael Heads (Wellington), Michael Dillon (Tal Tal), Carlos Lehnebach (Wellington), and Patricio Pliscoff (Lausanne). Of course the errors and misconceptions that may still exist are exclusively my responsibility.

In Chile, the project found early support in Dr. Belisario Andrade (Pontificia Universidad Católica de Chile) and Dr. Roberto Rodríguez (Universidad de Concepción). Once back in Chile, I can only express gratitude to the colleagues at the Pontificia Universidad Católica de Chile, which facilitated my incorporation as an assistant professor by means of a grant for young doctors. I am especially indebted to the Director of the Institute of Geography, Dr. Federico Arenas and the dean of the Faculty, Dr. José Ignacio González.

Field work in Chile during 2008–2010, especially for research on Asteraceae (Chap. 8), was supported by project Fondecyt Iniciación (2008) n° 11085016. Speaking about field work, long ago I learned from Calvin and Linda Heusser the "dirty side" of scientific field work. I will be always indebted to my old friends.

Vanezza Morales was a crucial helper in the final editing of most maps, and with computer programs like NDM/VNDM. I gratefully mention also the important advice provided by Tania Escalante (UNAM) and Claudia Szumik (U. de Tucumán). Giancarlo Scalera (Roma), and Carlos Le Quesne (Valdivia) kindly provided articles and figures. Sergio Elórtegui generously acceded to draw several original illustrations for this work and also contributed many photographs. Carlos Jaña helped finishing the most complicated figures. Sergio Moreira, Walter Welss, Hendrik Wagenseil, Jeff Marso, María Castro, Francisco Casado, and Carlo Sabaini kindly provided photos for illustrating this book.

Last but not least, I must acknowledge the life-long support of Mélica Muñoz-Schick and Sergio Moreira, who could transfer to me their passion for nature and beauty. Mélica, as ever, helped with the identification of species. Sergio also helped providing scanned images of botanical specimens, thanks to a grant to the National Herbarium provided by the Andrew W. Mellon Foundation trough the Latin American Plants Initiative (LAPI).

When the doctoral thesis was still a draft project, my way crossed the one of Paola, who soon turned to become my life companion. I would not have reached this goal without her continuous support. I could also not imagine that the relationship would be so fruitful: Sayén, Silene, Coyán, and Relmu remind me every evening that there are other important things in life than just writing books... there is also the possibility to read them!... especially when they deal not just with flowers but also with rabbits, bears, elves and fairies.

1 May 2010 Limache

Contents

Part I Geobotanical Scenario

Part II Chorology of Chilean Plants

Part III Islands Biogeography

Part IV Case Studies on Selected Families

Part V Where to from Here? Projections of Chilean Plant Geography

Abbreviations

AAO	Antarctic Oscillation
ACC	Antarctic circumpolar current
cfr.	Refer to
Chap.	Chapter
CONAF	Corporación Nacional Forestal
CONC	Herbario de la Universidad de Concepción
ENSO	El Niño Southern Oscillation
Fig.	Figure
GIS	Geographic information systems
ITCZ	Intertropical Convergence Zone
IUCN	International Union for Conservation of Nature
K/T boundary	Cretaceous/Cenozoic boundary
LDD	Long-distance dispersal
LGM	Last Glacial Maximum
m asl	Metres above sea level
mya	Million years ago
PAE	Parsimony Analysis of Endemicity
PDO	Pacific Decadal Oscillation
SEBA	Systematic and Evolutionary Biogeographical Association
Sect.	Section
SGO	National Herbarium Santiago, Chile
SNASPE	National public protected areas system
yr BP	Years before present

About the Author

Andrés Moreira-Muñoz was born in Los Angeles (Chile), studied at the German School in Santiago and graduated as Professional Geographer at the Pontificia Universidad Católica de Chile. Botanical interest was inherited from his grandfather and mother, both renowned botanists at the Museo Nacional de Historia Natural in Santiago. He obtained his doctoral degree in Geography from the University Erlangen-Nürnberg, Germany, under the direction of the plant geographer Prof. Michael Richter.

He currently occupies a position as assistant professor at the Instituto de Geografía, Pontificia Universidad Católica de Chile, and develops research projects about the chorology of Chilean plants, conservation biogeography and field-based education.

He is a member of several national and international associations like the Systematics and Evolutionary Biogeographical Association (SEBA), the Society for Conservation GIS (SCGIS), the IUCN Species Survival Commission, the Sociedad de Botánica de Chile, and Corporación de Investigación y Divulgación Científica Taller La Era (www.tallerlaera.cl).

Part I
Geobotanical Scenario

Chapter 1
The Extravagant Physical Geography of Chile

Abstract Current Chilean vascular flora and its biogeographical patterns are strongly related to the geographical features of the territory, past and present. Main characteristics of the physical geography of Chile are described, with emphasis on the geologic and climatic changes that affected the biome configuration since the Devonian onwards. Approaching the present time, the effects of the Pleistocene glaciations in the distribution of several communities are discussed.

Chile has been characterized as "a geographic extravaganza" (Subercaseaux 1940) due to its impressive geographical contrasts: it contains the driest desert on the planet, formidable inland ice fields, active volcanoes, fjords, geysers, a vast coastline and the major highs of the Andes.

The country stretches for 4,337 km along the south-western margin of South America from the Altiplano highs at 17°35′S to Tierra del Fuego, the Islas Diego Ramírez and Cape Horn at 56°S (Figs. 1.1 and 1.2). Chile's boundary to the west is the wide Pacific Ocean. The national territory includes several groups of Pacific oceanic islands, principally Rapa Nui (Easter Island), the Juan Fernández archipelago, and the Desventuradas Islands (Fig. 1.1) (Chap. 5). Besides this the nation has a geopolitical claim on a portion of 1,250,000 km^2 in Antarctica. Though geopolitical interests are beyond the scope of this book, and despite the modest presence of extant vascular plants in Antarctica (only *Deschampsia antartica* and *Colobanthus quitensis*), the Continent of Ice is of high interest regarding the origin of the Chilean plant world (Sect. 1.2, Box 9.1).

A. Moreira-Muñoz, *Plant Geography of Chile*, Plant and Vegetation 5,
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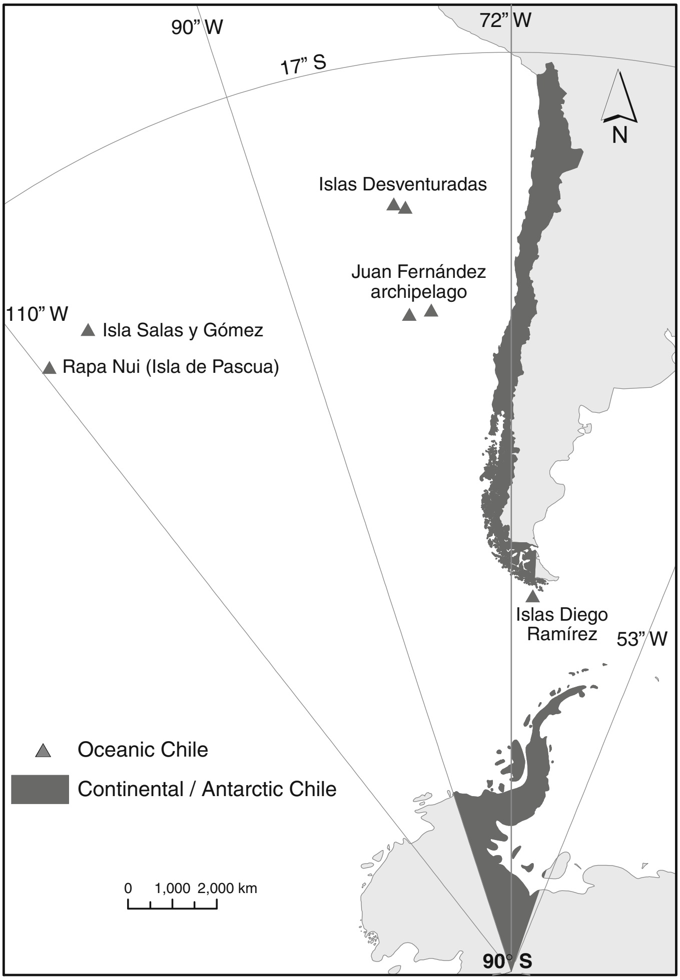

Fig. 1.1 Chile including the American continental portion, the Pacific islands, and Antarctic Peninsula. Polar stereographic projection with true scale at 71°S using ArcGIS 9. Base global map provided by ESRI Labs

The eastern margin of mainland Chile is the Andes cordillera, which reaches to a maximum of 6,962 m asl in the Monte Aconcagua at 32°39′S (Fig. 1.6). As its summit is located on the Argentinean side, the highest peak of the Chilean Andes is the Ojos del Salado volcano at 27°06′S, reaching 6,893 m asl. Contrary to the long latitudinal extent, in width Chile rarely extends more than 200 km, reaching a maximum of 360 km at Mejillones (23°S) and a minimum of 90 km at Illapel (31°37′S). The difference in altitude from the coast to the high Andes creates a series of bioclimatic variations in the altitudinal profile (Fig. 1.6). These variations, coupled with the climatic latitudinal gradient, create a variety of geographic conditions that dramatically

Fig. 1.2 Physical geography of Chile: **a** Valle de la Luna, Atacama desert, 23°S; **b** Cerro Las Vizcachas, Cordillera de la Costa, 33°S; **c** rocky coast at Concón, Valparaíso (32°50′S); **d** Laguna del Inca, Portillo, Andean pass to Argentina (32°50′S); **e** Glaciar Los Perros, Torres del Paine, Campos de Hielo Sur (51°S); **f** southern fjords and Cordillera de Darwin (55°S) (photo credits: **a**, **b**, **d**–**f** A. Moreira-Muñoz; **c** S. Elórtegui Francioli)

affect the Chilean vegetation from the arid North to the humid temperate rainforests in the South (Sect. 1.3).

1.1 Tectonics and Physiography

The main character of Chilean landscapes is driven by tectonic forcing: the geological evolution of Chile is related to the east-directed subduction of the Nazca Plate beneath the South American Plate (Pankhurst and Hervé 2007) (Fig. 1.3). The Chile Rise is an active spreading centre that marks the boundary between the Nazca Plate and the Antarctic Plate at the so called Chile Triple Junction (Fig. 1.3). The Nazca Plate is being subducted at a rate of ~65 mm/year (to the North of the Triple Junction), while the Antarctic Plate is being subducted at a slower rate of ~18 mm/year (Barrientos 2007). According to Ranero et al. (2006), the amount of sediments to the trench is variable in space and time: north of 28°S, due to aridity, there is a relatively small amount of erosion and sediment supplied to the trench; in the mid-latitude, the well developed river drainage system supplies much material to the trench; south of ~ 40°S glacial-interglacial periods might have controlled the amount of sediment supplied to the trench (Ranero et al. 2006).

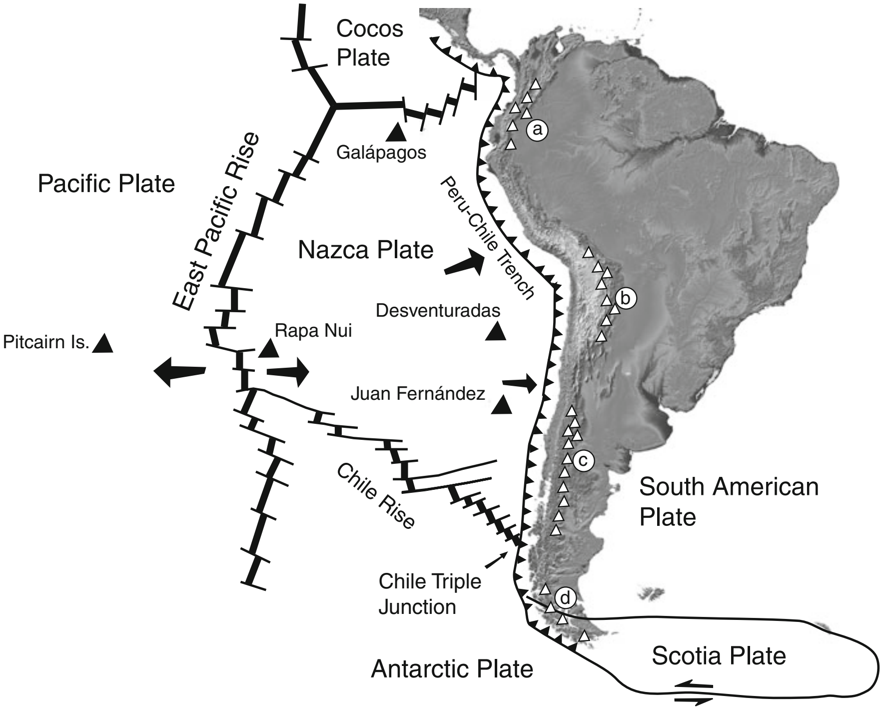

Fig. 1.3 Tectonic main features and volcanic zones of South America: **a** northern volcanic zone; **b** central volcanic zone; **c** southern volcanic zone; **d** austral volcanic zone (adapted from Orme (2007), by permission of Oxford University Press; see also Stern et al. (2007))

A prominent feature of the Nazca Plate is the Juan Ferrnández hot spot chain, a series of disconnected seamounts that disappear into the trench at 33°S (Ranero et al. 2006) (Fig. 1.3). Subduction is accompanied by intense magmatic and seismic activity (Orme 2007). Great earthquakes occur somewhere along the western South American margin every few years, and "no recorded human generation in Chile has escaped the damaging consequences of large earthquakes" (Barrientos 2007, p 263). Indeed, while writing these lines, on the 27th of February 2010, an earthquake with a magnitude of 8.8 followed by a tsunami affected Central-south Chile, resulting in hundreds of deaths and thousands homeless.

Together with earthquakes, the active volcanism along the length of the country is also a good reminder of the active tectonic processes acting below the surface (Box 1.1).

Box 1.1 Living Under the Volcano

Chilean active and inactive volcanoes comprise ca.10% of the circum-Pacific "ring of fire" (Pankhurst and Hervé 2007). These are mostly andesitic stratovolcanoes that occupy almost the entire length of the country, especially at the "South Volcanic Zone", that encompass most of the South American active volcanoes (Stern et al. 2007) (Fig. 1.3). More than 150 potentially active volcanoes have been detected, and 62 of them erupted in historical times (González-Ferrán 1994). One of the most recent is the eruption of Volcán Chaitén (43°S) on May 2008, which was responsible for the obligate abandonment of the homonymous town. The ash column reached a height of 15 km and spread wide upon the Atlantic (Figs. 1.4 and 1.5). Apart from its consequences and risks for human occupation, volcanism has been a constant source of disturbance in the Chilean ecosystems, especially in the southern temperate forests (Milleron et al. 2008).

1.1.1 Morphostructural Macrozones

Taking account of its tectonic and morphostructural features, Chile can be classified in a broad sense in five macrozones (Fig. 1.6) (Charrier et al. 2007; Stern et al. 2007):

(a) The Coastal Cordillera occupies the western part of the profile from 18°S to Chiloé Island (~ 42°S). It comprises the coastal batholith that consists predominately of Late Palaeozoic and Mesozoic igneous rocks, with paired belts of Palaeozoic metamorphic rocks cropping out south of Pichilemu (34°23′S) (Pankhurst and Hervé 2007). Very impressive is the high riffs ("acantilado") that stretches from 0 to 800 m asl at Iquique (20°S).

(b) The Central Depression is a tectonic downwarp with a Mesozoic to Quaternary sedimentary fill of volcanic, glacial and fluvial origin. This main agricultural

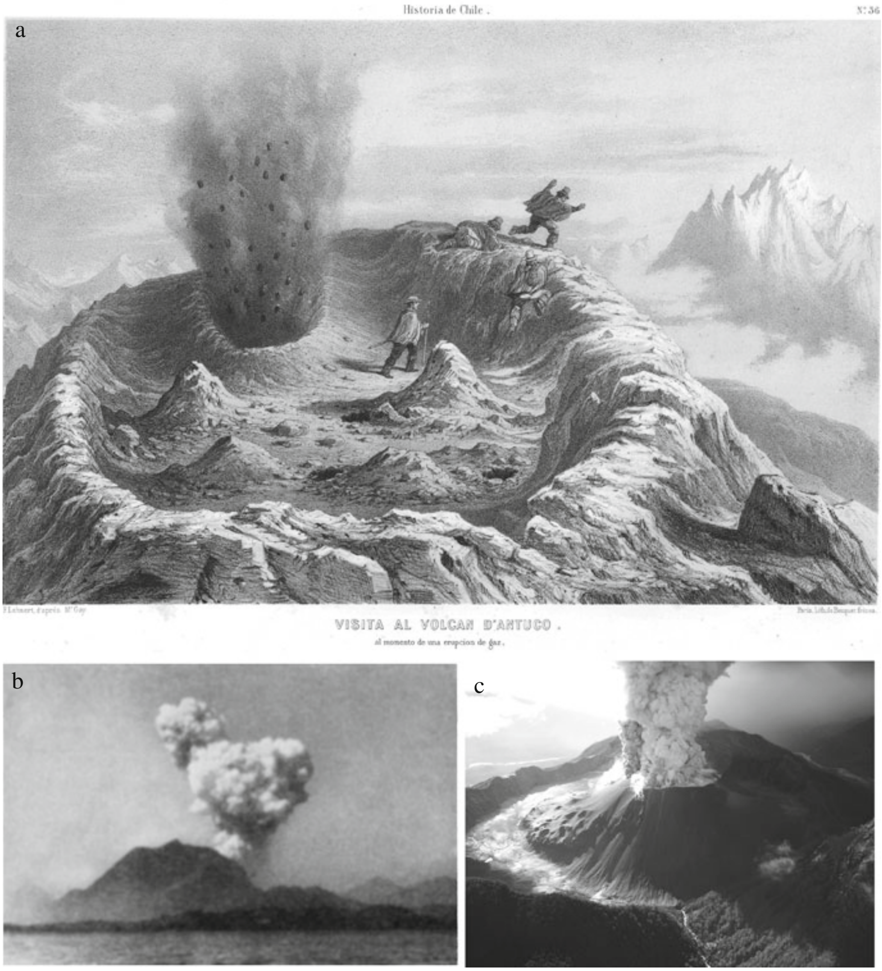

Fig. 1.4 Examples of volcanic activity in historical times: **a** ash expulsion by Volcán Antuco on the 1st March 1839, as represented in Claudio Gay's Atlas (Chap. 2); **b** eruption of Volcán Carrán in 1955 (from Illies 1959); **c** Volcán Chaitén eruption photographed on May 26, 2008 (photo by J.N. Marso, courtesy of the USGS)

and urbanized region ranges from 18°S to Copiapó (27°S), and again from Santiago (33°S) to Chiloé (42°S). It is absent between 27° and 33°S, in the so called zone of transverse river valleys or "Norte Chico" (Weischet 1970; Charrier et al. 2007). This zone corresponds also to the "flat slab" zone, a zone free of recent volcanic activity, associated to the subduction of the Juan Fernández Ridge (Fig. 1.3).

(c) The main Andean Cordillera is a chain of mountains that dates back to the Miocene, whose emergence continues today (see Box 1.5). It can be subdivided in three segments: Forearc Precordillera and Western Cordillera, between 18° and 27°S; High Andean Range, between 27° and 33°S (flat-slab subduction

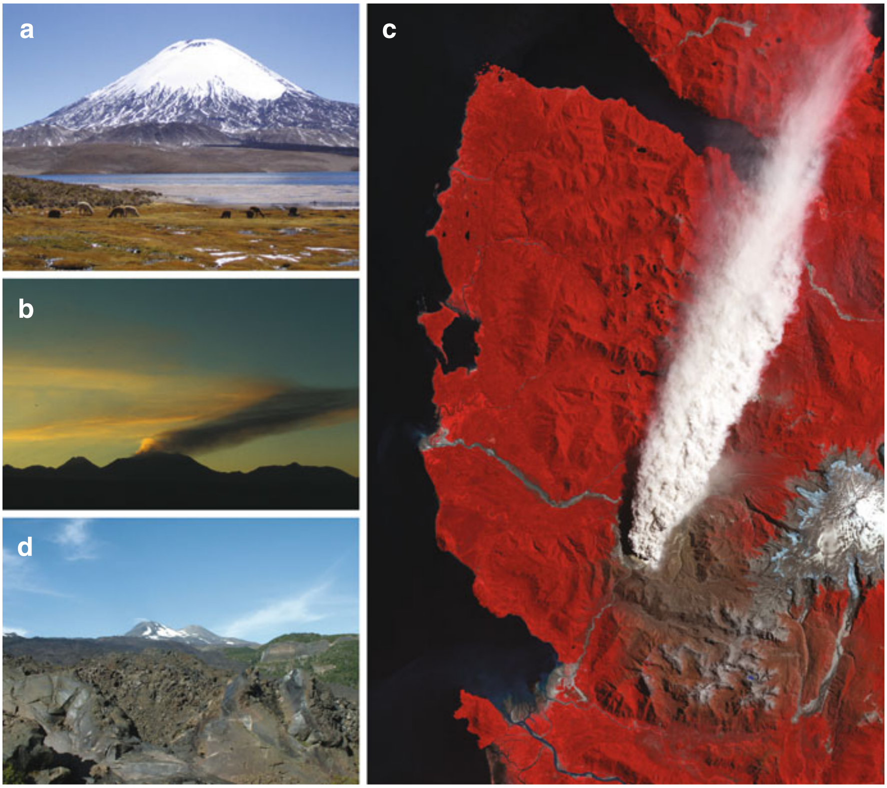

Fig. 1.5 Chilean volcanoes: **a** Parinacota volcano, 18°10′S; **b** steam expulsion of Volcán Lascar (23°20′S), on December 1996; **c** Volcán Chaitén (42°50′S), false colour Aster satellite image: plume of ash and steam advancing ca. 70 km to the north-east on January 2009; **d** lava fields around Nevados de Chillán (36°50′S) (photo credits: **a** H. Wagenseil; **b**, **d** A. Moreira-Muñoz; **c** NASA Earth Observatory (www.earthobservatory.nasa.gov))

segment); and Principal Cordillera, between 33° and ca. 42°S (Charrier et al. 2007).

(d) Patagonian Cordillera: the Andes' continuation right down into Tierra del Fuego at the southern tip of Chile, with a continuous reduction in height (Pankhurst and Hervé 2007). The origin of this low portion of the Andes has been related to an allochtonous Palaeozoic terrane (see Box 1.2). The west-southern margin of the land (42° to the South) is modeled by recent glaciations that carved the coastal areas into fjords and archipelagos comprising thousands of little islands (Pankhurst and Hervé 2007). It has been calculated that the coastal extension of Chile including these islands and southern archipelagos reaches 83,850 km! (IGM 2005).

(e) The Andean foreland of the southern Patagonian Cordillera or Magallanes basin consists of Upper Jurassic to Early Cenozoic sedimentary deposits (Charrier et al. 2007; Fosdick 2007).

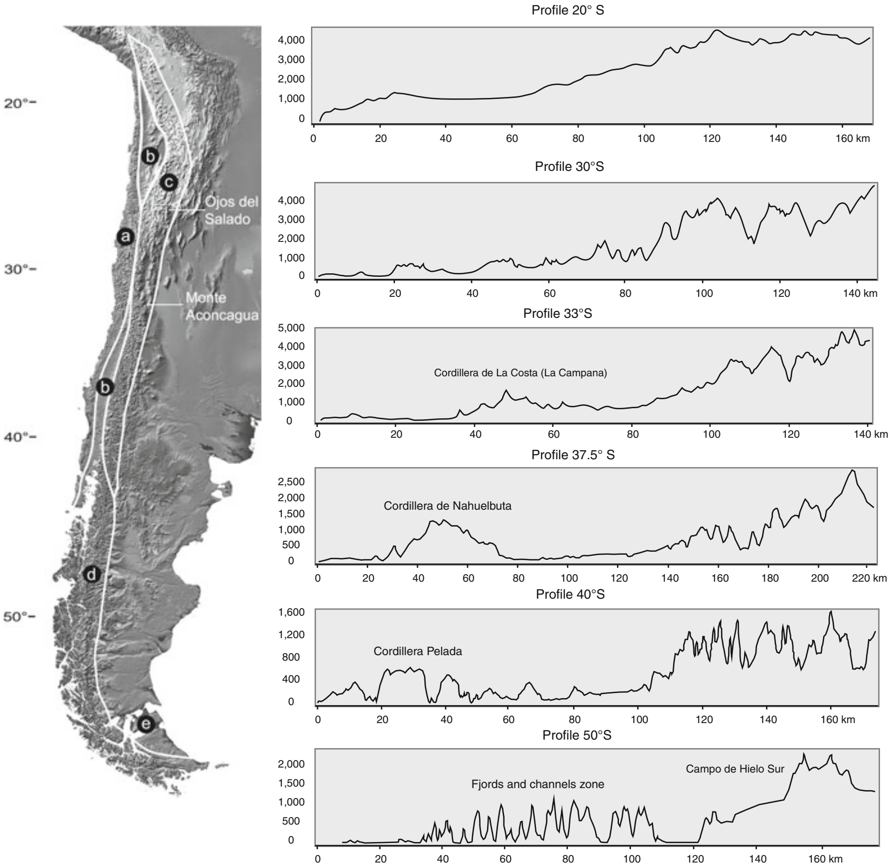

Fig. 1.6 Physiography of continental Chile, on the base of SRTM (Shuttle Radar Topography Mission) data (http://www2.jpl.nasa.gov/srtm/), five morphostructural zones (see text for explanation; for national political borders see Fig. 1.1). Altitudinal profiles have been produced with ArcGIS 9 based on Aster GDM data (http://asterweb.jpl.nasa.gov/gdem.asp). Note variations in the vertical scale, not homogeneous

Box 1.2 Patagonian Vicissitudes

The remarkable landscape and flora of Patagonia motivated early naturalists like the Perito Francisco P. Moreno to propose an independent origin of this microcontinent from the rest of South America (Moreno 1882, as quoted by Ramos 2008). The characteristic landscape and rocks led Moreno to remark strong affinities to other southern landmasses like Antarctica, Australia, and New Zealand, suggesting that Patagonia was the rest of a sunken continent.

This view was retained even during the time of continental drift discussion (e.g. Windhausen 1931). Current geologic and palaeomagnetic data suggests that indeed, Patagonia has seen successive periods of breaking and drifting during the whole Palaeozoic (Rapalini 2005; Ramos 2008). The TimeTrek model (see also Pankhurst et al. 2006) shows an amalgamation of Patagonia to Antarctic Peninsula during Late Carboniferous (300 mya), and a gradual separation from Antarctica into the Cretaceous (120 mya) (Fig. 1.7). Biotic exchange between South America and Antarctic Peninsula may have been favoured (and then prevented) more than just one time, following rather exchange cycles (Fig. 1.7).

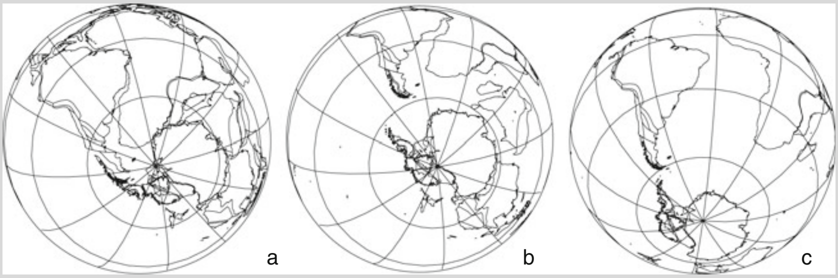

Fig. 1.7 Positions of Patagonia: **a** in the Late Carboniferous (300 mya) aggregated to the Antarctic Peninsula; **b** in the Early Cretaceous (120 mya), separated from Antarctica; **c** in the Eocene (50 mya), again close to the Antarctic Peninsula. Modeled with TimeTrek v 4.2.5, Cambridge Paleomap Services

1.2 Past Climate and Vegetation

Tectonic and geomorphologic processes, coupled with the oceanic-atmospheric system, have had enormous effects on the botanical evolution and its physiognomical expression (i.e. the vegetation). The main aspects of the palaeogeographical evolution of the territory will be resumed hereafter.

Palaeobotanical studies of Chile date back to Engelhardt (1891), Ochsenius (1891), Dusén (1907), Berry (1922a, b), Fuenzalida (1938, 1966) among others. More recent advances are centered in the Cenozoic (e.g. Cecioni 1968; Nishida 1984; Troncoso and Romero 1998; Hinojosa 2005). Constant improvement of the methods applied to the study of “climatically sensitive” sediments (e.g. coals, salt deposits, evaporites), together with studies in diversity patterns in global vegetation through time, are benefiting our understanding of the evolution of plant biomes in space and time (Willis and McElwain 2002).

The floristic and vegetational history of southern South America is strong related to the tectonic and climatic history of the *Gondwana* continent (McLoughlin 2001)

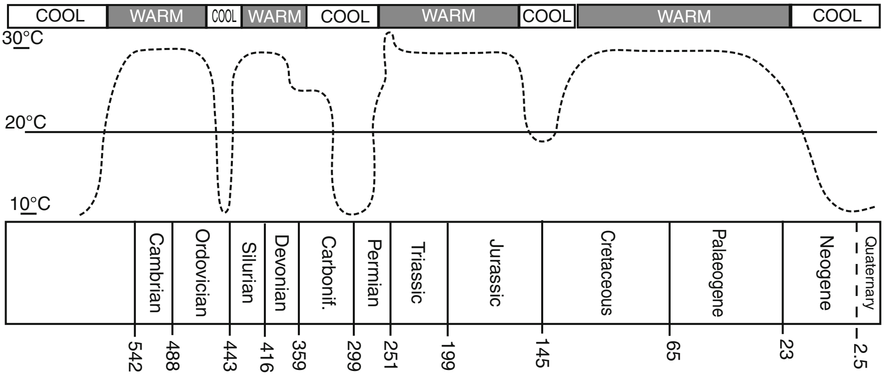

Fig. 1.8 Global climate change since the Cambrian onwards. Adapted from Frakes et al. (1992) and Scotese et al. (1999). Dates have been updated with the 2004 Geologic Time Scale (Gradstein et al. 2004)

(Box 1.3, Table 1.1). "During the 500 million years that Gondwana and its fragments existed, the Earth's global climate system has shifted from 'Ice House' conditions to 'Hot House' conditions four times" (Scotese et al. 1999) (Fig. 1.8). These global climatic fluctuations have constantly affected the biotic evolution and biogeography: floristic regions can be tracked back even to the mid-late Silurian, the time when according to most palaeobotanical evidence, the vascular plants have conquered the land surface (Willis and McElwain 2002; Raymond et al. 2006) (Box 2.3).

1.2.1 The Palaeozoic (542–251 mya)

Several orogenic events affected the western margin of Gondwana from the Late Proterozoic to the Palaeozoic (Ramos and Aleman 2000; Pankhurst et al. 2006). The Famatinian orogeny in the Ordovician (~490–450 mya) is characterized by the amalgamation of several allochtonous terranes, like Cuyania and Chilenia, implying that North America had collided with West Gondwana by that time (Astini et al. 1995). Mejillonia and Patagonia terranes amalgamated in the Early Permian, as the last convergence episodes (Ramos 2009) (Box 1.2). The development of preAndean foreland basins during the Palaeozoic, set the stage for the initiation of the Andes long before the event that culminated in massive Cenozoic uplift (Orme 2007). During the Late Palaeozoic, Gondwana became amalgamated to the supercontinent of Laurussia to form the vast single landmass called Pangaea.

From the Early **Devonian** to the Late Carboniferous (400–300 mya), global vegetation evolved from one dominated by small, weedy plants, only several decimetres in height, to fully forested ecosystems with trees reaching sizes of 35 m (Willis and McElwain 2002). During the Middle to Late Devonian (390–360 mya) warm, humid climates with high levels of atmospheric CO_2 prevailed worldwide, favouring the appearance of earliest arborescent forms of plants (see Box 2.3).

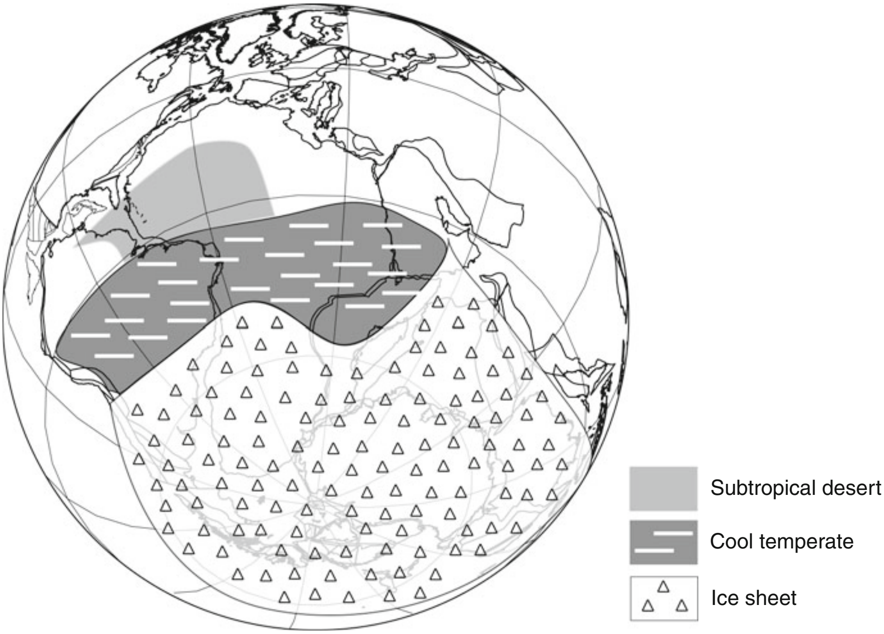

Fig. 1.9 Late Carboniferous biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

By the Late **Carboniferous** (330–299 mya) the southern flora consisted mainly of likely pteridosperms, lycopsids, Cordaites and Ginkgophytes (Vega and Archangelsky 1997). Diversity was rather low, and the southern flora was uniformly developed across Gondwana between 30°S and 60°S (Anderson et al. 1999; DiMichele et al. 2001). However, Cúneo (1989) suggests that floristic differentiation was also apparent on the west coast of South America. The presence of *Lepidodendron* and *Sigillaria* (lycopod trees) has been reported from the Carboniferous deposits of Chile (Charrier 1988). Late Carbonifeous ended in a widespread glaciation, one of the most severe in Earth's history. The Permo-Carboniferous glaciation (310–290 mya) lasted for around 30 million years (Beerling 2002); Gondwanan continents were locked in deep glaciation (Fig. 1.9).

The **Permian** (299–251 mya) was characterized by major global climate changes, from glaciated (icehouse) to completely ice-free (hothouse) stages (Fig. 1.8). "With the onset of glaciation in the Permian, the flora changed dramatically with the appearance of *Glossopteris* and the disappearance of most of the Late Carboniferous elements" (DiMichele et al. 2001, p 467). By the Middle Permian, one of the most striking vegetation changes was the relatively increased proportion of seed plants together with a reduction of the swamp-dwelling lycopsids and sphenopsids (Wnuk 1996, McAllister Rees et al. 2002). *Glossopteris,* a gymnosperm genus with many species, turned to be the characteristic plant of Gondwana (DiMichele et al. 2001). Indeed, *Glossopteris* dominant presence across Gondwana

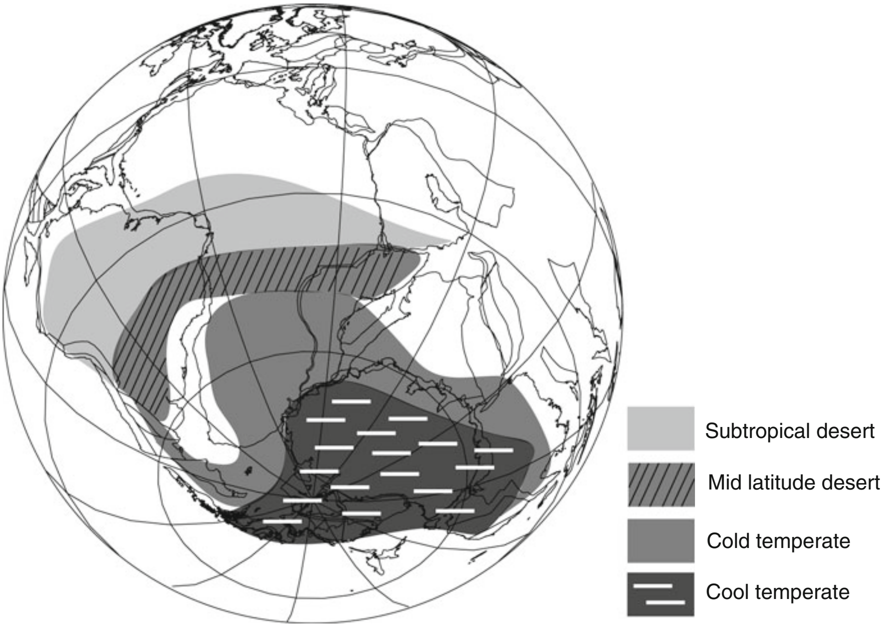

Fig. 1.10 Middle Permian biomes (adapted from Willis and McElwain (2002) on a TimeTrek 4.2.5 model, Cambridge Paleomap Services)

is one of the keys that supported the continental drift theory of Alfred Wegener. *Botrychiopsis*, another typical species from west Gondwana, went extinct when the environmental conditions typical of a greenhouse stage were created by the end of the Permian (Jasper et al. 2003).

The Permian flora of Gondwana was significantly more diversified than the one of the Late Carboniferous (Cúneo 1989), and the floristic provinciality changed during the course of the Permian. The belt located between 60° and 45°S in western Gondwana was called the "Southern temperate semiarid belt of middle latitudes", characterized by *Glossopteris* and moderately thermophilic vegetation with abundant tree-ferns and lycopods (McLoughlin 2001; Chumakov and Zharkov 2003) (Fig. 1.10).

1.2.2 The Mesozoic (251–65.5 mya)

The transition from the Palaeozoic to the Mesozoic is characterized by a dramatic event: the Permian-Triassic extinction event, which apparently saw the destruction of 90% of marine life on Earth due to extensive volcanism, under other causes (Benton and Twitchett 2003). The impacts on the terrestrial ecosystem were not so drastic, or paradoxically even favorable for some plants (Looy et al. 2001).

The **Triassic** (251–199.6 mya) climate was relatively warm compared to today, and continentality and aridity were more extended due to the permanence of the