Evolution of the Arborescent Gymnosperms: Pattern, Process and Diversity

Volume 1: Northern Hemisphere Focus

The arborescent gymnosperms are the most prevalent trees in one-third of the world's forests, and have dominated the Earth's forest ecosystems through much of evolutionary time. They encompass over 70 living genera and nearly 700 species of evergreen conifers and related trees, and include the largest and longest-lived organisms on this planet. This two-volume treatise provides detailed descriptions of each genus based on first-hand surveys of their structure, adaption, ecology, function and development. It also incorporates evidence from molecular studies, palaeobotany and environmental data to provide a holistic understanding of their overall evolution and diversity. Covering the world's temperate and tropical forests, Volume 1 principally focuses on Northern Hemisphere genera while Volume 2 covers those with a predominantly Southern Hemisphere range. Together, the set provides a comprehensive, global reference for researchers in palaeobotany, plant science, geobiology, evolutionary biology, ecology and plant genetics, as well as arboriculturists and conservation managers.

Christopher N. Page (1942–2022) held a first class bachelor's degree in geology and a PhD in cytogenetics. Following positions at the University of Queensland and University of Oxford, he joined the Royal Botanic Garden in Edinburgh as a specialist tree scientist. This provided him with a base for half a century of global study of conifers and ferns, including more than 10 cumulative years spent in the field on every continent except Antarctica. After leaving Edinburgh, he joined the University of Exeter in his retirement, where he continued to study ancient plant groups by integrating multi-sourced plant data with phylogenetic arrays. The author of 8 books and 150 journal papers, Dr Page was best known for bridging fields as diverse as geology, palaeobotany, evolutionary biology, biodiversity, genetics and modern molecular studies in order to develop environmental–evolutionary interpretations and applications. He was awarded two scientific Gold Medals – fittingly one for plant biology from the Indian Pteridological Society and one for geology from the Royal Geological Society of Cornwall. This treatise on gymnosperms, the manuscript for which was completed shortly before his death, is the culmination of 54 years of research, teaching and field study.

'This is truly a magnum opus by a world expert on the conifers, and it has been fascinating, enjoyable and informative to read. It is based on the extensive travels of the author to everywhere that arborescent conifers grow. This has enabled the author to illustrate it with a wonderful collection of his personal and most informative photos of the conifers of the world. The text is a skilful combination of data from palaeobotanic, molecular and field observations that show the history, evolution and contemporary status of this vitally important group of plants. It is the author's personal experience with each genus and familiarity with so much of the literature about conifers that makes this such interesting reading. There is no doubt that this book will remain a classic on the subject for many years to come.'

Professor Sir Ghillean Prance FRS

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Preface and Acknowledgements

Mission Statement

I have been honoured to develop scientific interests that span from the biology and functioning of living plants, to geological history and the Earth sciences aspects of their forbears, to evolve interpretations of plant and vegetation evolution and dynamics on this planet, founded in ecological reality, direct long-term cultural study and experimentation. In treading such a dedicated path across decades, direct ecological forest contact with living members – as long-lived forest trees in multiple habitats across the Earth – plus subsequent cultural, laboratory and experiment study and recording, I have everywhere expanded on the detail of their structures, life-history dynamics, adaptive trends, functioning and environmental relationships, which were often previously little-known. I thus present throughout this book understanding of how they have each evolved and succeeded through long periods of past geological time, with my focus especially on where and how living ancient plants occur, and their survival dynamics, processes, environmental interactions and attainments. *Pattern*, *process* and *diversity* are vital components echoed throughout, the first two closely reflecting how evolution largely happens, while diversity is its recurring outcome. All these studies have taught much, and served to build factual bases of biological reality from which pictures of evolution – touching and interacting variously and dynamically within wider external influences, especially of environment and change – begin to more precisely emerge. Bridging these fields, and utilising the standpoint of living ancient members, has been a rewarding and ever-developing challenge, in which I think I have achieved a quite unique groove. Here we strengthen our understanding of reasons for these species' survival in the present, and how we can use this information to best promote and conserve their existence in the future. Recording and enlarging on all of these aspects through every known genus of living arborescent gymnosperms is the purpose of this book.

Background and Approach

I have been fortunate to have had a family background in aviation. My family were aviation engineers in the UK, and founded one of Britain's (and the world's) first aeroplane-building companies. My 'family firm' built the HP42, Britain's main long-haul airliner of the time, which successfully served long-distance British airline passenger routes across the Old World throughout the 1930s. Later, my father, working with a different aircraft company in Gloucester during the Second World War, helped to design and build the world's first jet engine, to which I believe his contribution was the development of its turboshaft core. Family conversations were always about engineering.

But although I was a great disappointment to the family in becoming a scientist and not an engineer, nevertheless it was from an early age that the sheer complexity of aeroplane construction greatly influenced me. Aircraft structures then notably offered many serially repetitive shapes and elements, placed as repeating series through multiple sequences and scales. These then became organised into complex, specific but integrated roles, the sum of which became an organised whole, with distinctive shapes, curves and purposes. I could only marvel at these assemblies as a boy. I later learned that these assemblies, formed into multiple complexities and purposes, contributed great strength with lightness in weight and efficient materials utilisation. It was these many recurrent engineered shapes that offered similar perspectives in their oft-repeating patterns to those I could see also in many ways in nature, including in the fossils I collected as a boy (from Jurassic ammonites to Carboniferous horsetails and ferns) and their modern living counterparts. Nature, I thought, was doing this first, even before those first massive airliners had been designed! These perspectives captured my young imagination. I thus attached myself through this route to both fossils and living plants, and the transformation of one to the other that had taken place, about all of which I wanted to discover more. Of these ancient plants in particular there was thus a great detail to be learned about structures, purposes and the steps of their development by gaining an understanding of what was living around me today. On seeing my fossil collections, I was impressed by words of wisdom received, as a boy, in a memorable conversation with the scientist Dr Jacob Bronowski, a colleague of my father. He saw my collections and encouraged me to become a scientist – guidance I still clearly remember and still accord, and I have never looked back.

It was thus logical that when I went to university in what seemed like a lifetime later I was ready to study geology. With a BSc First then gained in one scientific topic, I was able to specialise for a PhD through the mid-1960s in another: cytogenetics (as you do if you start off as a geologist!). Few of my contemporaries could understand what geology and cytogenetics had to do with each other, but to me they spanned the width of my interests – each, for me, were complementary gateways to the study of evolution, each approaching the same logical topic from opposite directions and scales. The former embraced studies of macro-scale actualities of evolution through long geological timescales as recorded in the rocks, to learn about the processes and circumstances by which these came to be. Both also added dynamism.

Even more, new ideas were being initiated around me. In Newcastle, a new topic of palaeo-magnetism was beginning to provide evidence that the continents of the Earth had not always been where they are today (so I lapsed a bit into the physics of what became Earth sciences as well). So dynamics came into the geological picture, and pre-war studies of movements of continents, by which I was already fascinated, were coming back to life. By comparison, cytogenetics offered evolutionary principles of its own, which were also of dynamics, at the micro-scale. These showed how life functioned and developed as living things. Its chromosomal mechanisms demonstrated how the fundamental building blocks of living organisms contributed to the dynamics of evolution. I studied especially the roles and interplay of hybridisation and polyploidy, and found processes of life actually evolving in front of me! Each of these two active backgrounds, Earth sciences and cytogenetics, provided solid but dynamic cornerstones.

Focusing on ancient plants as recorders of long evolutionary time, I especially studied horsetails, ferns and arborescent gymnosperms. Here, the sum of arborescent gymnosperms of the Earth form the core of this book. These trees are here also informally termed the 'resinifera', for there is no other single term that includes all of the 'conifers and their relatives' in the broadest sense, living and fossil. I thus pioneer several further new words. You may feel that, at first sight, such mostly evergreen trees and the forests which they form have a remarkably poor image. This is an image abundantly propagated by forestry plantations worldwide, of monocultures of dense trees planted in close and serried ranks for mass production of softwood timber. Within such plantations little, if any, light is devised to penetrate, and any other vegetation or wildlife is sparse. Such an image of 'conifers' is widespread, but this image is the equivalent of judging the world's bird diversity, from swans to hummingbirds, from ostriches to kingfishers, from albatrosses to wrens, from eagles to robins, and from penguins to lyre birds, merely from knowledge gained from a single glimpse inside an artificial battery chicken house, equally containing monocultures of serried ranks of production-line chickens, and into which little daylight penetrates! Such nightmare experiences, whether of plantation trees or chickens, have extraordinarily little to do with the *true biology of evolution* of the plants and animals respectively represented, when compared with the extraordinary *natural diversity* of each that occurs in the wild. In the case of these trees, as in that of the birds, they exist often with amazing diversity, exhibiting across long lifetimes considerable magnificence and venerability. They also include many of the tallest and oldest living organisms on this planet. As I attempt to show here, they are also little-appreciated but also vitally important evolutionary guides through time, and upon their evidence we can begin to deduct wider perspectives, including of the distant past, and also extrapolate this information to the present and to survival in the future.

If we take a different perspective, a different picture builds. In eastern Asia resiniferous trees are treated differently. Many are seen as positive icons of the wild landscape, appearing often as prominent elements in landscape art where they integrate dynamically into the tapestries of especially rocky mountain landscapes. In cultivation, trees are each given space to grow and develop their own, often wide, characteristic crown shapes of distinction. Cragginess develops with age in many, and is individual to different genera, which are appreciated for their own worthiness and reverence, especially those of the great age that individuals often achieve. They become consequently revered as symbols of strength, longevity and steadfastness. Their mature forms are often likened to dragons – a perspective which ironically reflects the palaeo-origins of many in relation to dinosaurs, of which these are the equivalents, but which are still alive! Certain crown forms convey messages, with large, laterally growing boughs seen as stating a greeting of 'welcome' to those who approach. The visual perception reflects their biological reality as organisms that have evolved as integral and functioning components of the landscape at large, which between genera and environments are constant and subtle lifetime interactions and records.

This book was originally made possible by the advent, when I started as a student in the early 1960s, of long-distance jet air travel. Well, if my family built the aeroplane, and my father developed the jet engine, their use seemed to be an inherited consequence! Travel extensively then allowed me, over the decades since of logging 133 long-haul flights, and local ones I have flown myself, to have accessed and worked in wild forests of all types, from Alaska to Patagonia, and from Siberia to Tasmania, and through vastly many areas of the tropics and Southern Hemisphere. Much of the basis of this book has then been garnered through field-trekking with many experienced foresters through many of the world's mountains and forests (sometimes involving activities which I have never been really sure my travel insurance policies strictly covered!). This became a quest, which also built upon strong fossil histories. For through sustained interest in ancient living plant dynamics, I have developed pictures of relationships between structures, adaptations, functions, patterns, processes and environments. All have also included interests spanning from

genetic control to the actualities of diversity, seeking wherever possible additional information from independent sources, including especially palaeobotanic and geological ones, and today embracing also cytogenetics, molecular studies and those of Earth systems dynamics. I have always used professional taxonomy in verification of materials I have collected and studied, and from this basis, I have developed routes from which to approach backgrounds of evolution. My own strong interests in adaptive and functional steps in relation to environmental exactitudes, through first-hand observation of forest environments across the globe for more than 50 years, interlinking plant distribution, ecological achievements and tolerances, and the dynamics and interactions of forest presence with geomorphological processes and geology, has become a quest.

At a more personal level, I could not live without plants. And this means not just in a static sense, but very much a dynamic one too, with their ever-present development and change, maturity and turnover, and the patterns and processes involved and the sheer diversity of life that is the outcome. Throughout I am fascinated by observing, recording and photographically memorising, with opportunities to delve into modest cultural experimentation and feed back results to further understanding of wild ecosystems, sometimes in great detail. I am strongly aware of the immeasurable and multifaceted contribution that these plants are making to the well-being of the planet's global environment. In this, I am especially fortunate to have lived a life in fullest appreciation of these goals, and fullest utilisation of opportunities to encounter those dynamics and that diversity on a global basis.

I often reflect on a statement of the Welsh author W.H. Davies, who said 'What is this life, if full of care, we have no time to stand and stare.' It can be the most important time we ever spend. In consequence, much of what I offer across this book is data gathered first-hand. Within this, for each genus, perceptions then arise of the many detailed forest components, sub-components, interrelationships, interactions, species diversity and niche specialisations of each plant, yielding dynamic pictures of evolutionary patterns, processes, balances and dynamics of forest presence, and their contribution to environmental balances, through widely varied ranges of scales, organisms and circumstances. Much of the field data has been largely first-hand collected on my own treks through temperate and tropical forests across the globe. First-contact in the field with each living genus has always been memorable. It has also been utterly dwarfing to stand among the tallest and oldest living organisms on this planet and to witness their cathedrellian dimensions. It has also been immensely humbling to shake hands with the oldest individual living plant known, already more than 2,500 years old when Christ was born. Each point in a forest is an ever-changing tapestry. Stay and watch. So many things are placed as if with structural precision, but also surprisingly interdependent upon one another. Appreciate the many subtleties, interactions and the stages of each plant and other organisms, and their often intricate adaptations and survival strategies. Everything has its place, functions and contributions. Only by sitting quietly on a log and looking around do you even begin to understand the presence of their interdependencies and complexities. This has opened opportunities to access most genera across their wild habitats and the environments to which they are adapted. Climbing their mountains and seeing seasonal changes, habitat diversities and often peculiarities, gaining close encounters through climbing the trees in the field in search of cones with seed which, documented and authenticated, has then accompanied me carefully back for experimental cultivation. The data for this book, has, therefore, not been compiled in haste. An abiding memory is that each time I have seen a new genus or member of a genus in a new site, I have learned something new! All are important in understanding how the present begins to provide unique 'windows' of inference and interpretation in relation to both the past and the future.

In so doing, to accommodate knowledge of the full spectrum of form and function consequently and recurringly evolving within living plants, in a paper I wrote and which was refereed in 1976 – and finally published in a joint volume three years later – I introduced the word 'diversity' to biology. This contribution has subsequently become my most quoted paper. The word 'diversity' in the title summarised my appreciation of the biological perspective that the breadth of richness that knowledge of the evolutionary outcomes of these plants engenders: their structures, patterns and processes, the width and variety of their adaptations, environmental placements and applications achieved. This was a concept that I believe Darwin also especially appreciated, and which shed much light on his thinking, although I am not aware that he actually used the word 'diversity' itself. My introduction of this word to biology has subsequently been adopted widely, and thus perhaps remains one of my own chance enduring contributions.

Building on this living plant approach to understanding evolution in ancient vascular plants, it has become a recurrent particular pleasure to bring matured views on processes, structures, functions, environmental interplays and adaptive significances in relation to taxa – and the consequent diversity – to evolutionary meetings and symposia. At these I tend to especially meet and enjoy listening to my many learned palaeobotanic colleagues, who I see 'coming the other way'. Their palaeo-information is direct information, and often carries important minutia of detail. Mine is more holistic and interpretive, and extrapolates from the present to the past, drawing possibilities, principles, significances and approaches, especially the 'why' and 'how' of the dynamics of evolution.

In pursuit of gain of this living plant approach, clearly travel opportunities to make direct contact with real-life vegetation in the field has always been a basic component. This has given me opportunities for collection of authenticated and located living materials, which have then yielded further information as studies have progressed, developed and matured. These have shown the stages of structures, processes and

development not usually seen in the field, for they can be brief, ephemeral and occur most often only high in the canopy of forest trees in the wild.

Across the last 50+ years, travel has remained integrally important to the founding and development of this research programme. I thus especially feel that many airlines deserve respected acknowledgement for my safe conveyance as important background contributors to this quest, as was the ship *The Beagle* to Darwin. I thus acknowledge and thank the following airlines, who have been my major conveyors (names at the time of using): B.O.A.C., British Airways, British Caledonian Airways, Brymon Airways, Dan Air London, Monarch Airlines, Air 2000, Air UK, Fly Be, Aer Lingus, K.L.M. Royal Dutch Airlines, Air France, Union Transportes Aeriens (UTA), TAP Air Portugal, Alitalia, Aviaco, Air Azores, Iberia, Meridiana, Malta Airlines, Air Europe, East African Airlines, Air India, Indian Airlines, S4 Siberian Airlines, Asiana Airlines, China Airlines, Japan Air Lines, All Nippon Airways, Toa Domestic Airlines, Nihon Kinkyori Airways, Japan Asia Airways, Cathay Pacific Airways, Malaysian Airlines, Singapore Airlines, Philippine Airlines, Thai Airways International, Air Niuguinea, Quantas Australian Airlines, Trans-Australian Airlines, ANA Ansett Airlines, Air New Zealand, New Zealand National Airways, Air Caledonie, Air Pacific, Polynesian Air Ways, South Pacific Airways, Fiji Airlines, Island Air, Alaskan Airlines, Canadian Pacific Airlines, Continental Airlines, Pan-American World Airways, Delta Air Lines, Eastern Air Lines, American Airlines, Ozark Airlines, Piedmont Airlines, Southeast Airlines, Air Atlanta, Air Florida, Atlas Air, Virgin Atlantic Airlines. Journeys in several smaller light aircraft to remote field sites have also been widely utilised.

Developing directly from these travels, this book then embraces research stimulus and experience gained through successive periods at many universities and other academic bases across half a century. Travel throughout has been supported by my making 20+ overseas university lecture tours (visiting every continent except Antarctica), and has permitted the gain of much local knowledge. Several additional trusts and foundations have provided direct research support, including especially: The Leverhulme Trust, The Nuffield Foundation, The UK Sainsbury Trust, The Standley Smith Trust, UK Science Research Council, UK Natural Environment Research Council and NATO. Additionally, the Conifer Conservation Programme – which I founded in April 1971 from the Royal Botanic Garden, Edinburgh, and which now forms one of the longest-running conservation programmes in the world – also provided a core around which much additional evolutionary spin-off study could progress in its support. Further, I wish to acknowledge with enduring gratitude the generous financial support of a UK Leverhulme Trust Senior Fellowship towards final assembly of especially diagrams and photographs for this book. To all, I hope that the final outcome offers some positive return. Contributors include: Royal Botanic Garden Edinburgh, Royal Botanic Gardens, Kew, Forestry Commission UK, University of Cambridge, University of Leeds, The Linnean Society of London, The Royal Horticultural Society, The British Library, The Royal Geographical Society, Natural History Museum London (Botany and Geology sections), Indian Forest Service, Dehra Dun, CSIR – National Botanical Research Institute, Lucknow, Botanical Survey of India, Eastern Regional Centre, Shillong, Japan Forestry Agency, University of Tokyo Botanical Gardens, University of Tokyo Department of Forest Science, Sapporo University, Yakushima Forest Service, Tomsk State University, Novosibirsk State University, University of Hong Kong, Taiwan Forestry Bureau, National Taiwan University, University of Manila, Philippines Forestry Management Bureau, University of Queensland, Queensland Department of Agriculture and Fisheries, Queensland Parks and Wildlife Service, CSIRO Canberra, Royal Botanic Garden Sydney, University of Tasmania Department of Biological Sciences, University of Auckland School of Biological Sciences, University of Christchurch School of Biological Sciences, Department of Scientific and Industrial Research (DISR) New Zealand, Laboratoire de Botanique et d'Ecologie Végétale Appliquées de Nouméa, University of the South Pacific Suva, Samoa College Upolu, Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM) Papeete, Bishop Museum Honolulu, US National Park Service, US Fish and Wildlife Service, US Department of Agriculture Forest Service, University of Washington Seattle, University of Colorado Boulder, University of West Florida Pensacola, Duke University North Carolina, George Mason University Washington D.C., Smithsonian Institution, New York Botanical Garden, Corporación Nacional Forestal Chile, Universidad de Chile Santiago, Universidad Austral de Chile Valdivia.

Through all my travels I have always carried a camera (usually at least two), and with all resulting presentations I have taken the philosophy that illustrations can 'say a thousand words', but also that illustrations should be complementary and additional to that which can be described in words. Much source material has been in native wild forests, but additionally in Britain, Ireland and Western Europe full opportunities for further close-up studies have followed individual tree developmental studies, especially on 'captive' specimens at the following locations: Abbotswood Gardens, Adelaide Botanic Garden, Alnwick Castle, Altyre Estate, Arboretum de Villardebelle, Arboretun des Barres, Ardkinglass, Ardvorlich, Barbarano, Bardolino, Batsford Arboretum, Bedgebury National Pinetum and Forest, Belsay Hall, Benmore Botanic Garden, Berne, Beziers, Bicton Botanical Gardens, Birr Castle, Blair Atholl Estate, Blairquhan, Boconnoc, Bodnant Garden, Bolderwood, Borde Hill Garden, Bowood House & Gardens, Brodick Castle Gardens and Country Park, Buckfast Abbey, Burncoose, Caerhayes Castle, Cambridge Botanic Garden, Cannop, Carclew, Castle Kennedy Gardens, Castlemilk, Cheltenham

Parks, Christchurch Botanic Garden and Arboretum, City of Bath Parks, Clinton-Baker Pinetum, Coldrennick, Colonsay House, Cothele, Cragside, Crarae Gardens, Culzean Castle, Curraghmore, Dawyck Botanic Garden, Dehra Dun Forestry Arboretum, Des Barres, Desenzano, Dropmore Park, Drumlanrig Castle, Dunkeld, Dunloe Castle, Durris House, Eastnor Castle & Gardens, Endsleigh, Enys Gardens, Exbury Gardens, Fota Estate, Garda, Gardone, Garinish Island, Gillywood, Glendurgan Gardens, Glen Kinglass, Gloucester Parks, Halgarrick Lodge, Hardwicke Hall, Headford, Heligan, Hergest Croft, The Hermitage, Highnam Court, Hijuela del Botanico Orotava, Hilversuum Bleidenstein Arboretum, Hopetoun, Howick Estates, Ickworth Estate, Ilnacullin, Inverary Castle, Isla la Garda Arboretum, Jardin Botanico Funchal, Jardin Botanico Puerto de la Cruz, Jardin Botanico Tafira Alta, Jardin des Plantes de Museum National d'Histoire Naturelle Paris, Jardin Monte Palace, Jardins Quinta do Imperador, Keir House, Killerton, Kilmacurragh, Kilmun Arboretum, Knightshayes Court, Kyoto Gardens, Lake Garda Arboretum, Lamellan Estate, Lamorran, Lanhydrock, Leonardslee Gardens, Limoges, Logan Botanic Gardens, Lucknow Botanic Garden, Lyon Arboretum, Maderno, Malahide, Manerba, Melbourne Botanic Garden, Montpellier, Morrab Gardens, Mount Congreve Gardens, Mount Edgcumbe, Mount Field Botanic Garden, Mount Stuart House and Gardens, Mount Usher, Muckross Abbey, Murthly Castle Narbonne Parks, The National Botanic Gardens of Ireland, Nettlecombe Court, Nymans Gardens, Oxford Botanic Garden, Palheiro Gardens, Paris Parks, Parque Santa Catarina, Pencarrow, Penjerrick, Periigueux, Pine Lodge, Powerscourt House and Gardens, Powis Castle, Quimperle, Quinta Palmeira, Quinta Vigia, Quinto do Santo da Serra, Rhine Valley Arboretum, RHS Wisley, Rosewarne, Ross Priory, Rossdohan, Rowallane Garden, Royal Botanic Garden Edinburgh, Royal Botanic Garden Sydney, Royal Botanic Gardens, Kew, Scone Palace, Scorrier House, Sheffield Park, Sherborne Castle, Singleton Park, Sir Harold Hillier Gardens, Sirmione, Smeaton House and Gardens, Speech House, St. Erth, St. Marlow, Stanage Park, Stanway, Stourhead, Strathallan, Streatham Hall, Strete Ralegh, Strone Castle, Sydney Botanic Garden, Talbot Manor, Taymouth Castle, Tokyo Botanic Garden, Trebah Gardens, Tregenna Castle, Tregrehan Garden, Trelissick, Trelowarren, Tremenheere, Tremough, Trengwainton Garden, Tresco Abbey Gardens, Trevince, Trewardretha, Tyninghame Estate, University of Exeter Estates, University of Reading, University of Washington Arboretum, Verona Parks & Gardens, Verona, Vittoriale, Wakehurst, Warnham Court, Werrington Park, Westonbirt|The National Arboretum, Windsor Great Park.

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Enduring appreciation must especially go respectively to experience gained from the late Dr Len Brass and the late Dr Tim Whitmore, who have each (themselves a generation apart) been my unofficial tropical expedition mentors. Further in-depth library work has formed an extremely important additional final part of this book's survey, in keeping my own ideas up to date in wider research perspectives. For this, I have intensively searched many different UK libraries. Indeed, in some UK libraries, which represent some of the best scientific and botanical libraries in the world (notably the library of the Royal Botanic Gardens, Kew), I am regarded as virtually a fixture! Further, specialist technical help is also gratefully acknowledged from several sources, which especially include Mrs Jane Clare Page, Mrs Valerie Waggott, Dr Mami Yamazaki, Mrs Yelena Zueva, Dr Nadia Bystriakova and Dr Yuri Ivanenko, each for careful translation of respective literature from languages beyond my own knowledge. Technical computing support from John Muteham has positively resolved many major computing catastrophes. The text of this book has then been composed very largely to a background of musical symphony, especially by that of *Piotr Olich Tchaikovski*, whose rhythmic projections fired many distillations of my own constructive imagination. Artwork support from two of my daughters, Zoë Page and Tamsin Page, is also respectfully acknowledged. Enduringly, I acknowledge too that my daughters Zoë Page, Erica Page and Tamsin Page have been of invaluable practical help every time I became baffled by minor computing technicalities. I also offer thanks to my wife, Clare Page, for her long-suffering stoic support of this book's steady preparation.

Finally, there is also an extraordinary, and almost haunting, coincidence of circumstances of location of preparation of the text of this book in a nearly thousand-year-old cottage in west Cornwall, UK. Unknown to me when I originally retired here, I subsequently found that when Charles Darwin returned to Britain from his global circumnavigation on *The Beagle* on 20 October 1836, his ship first docked at nearby Falmouth. Darwin and Captain Fitzroy then both spent their first nights back ashore. Darwin stayed at the estate house for which this cottage was then that of the estate manager. Darwin is said to have brought with him living plants on *The Beagle*, which were subsequently brought to this cottage for onward planting. That Darwin and his plants likely trod the path of this cottage nearly 200 years before my own residence here offers a strange echo of pre-ordainment in its unheralded coincidence.

Christopher N. Page,
Cornwall,
April 2022

Post-Script

Very sadly Chris passed away in December 2022, just as his lifetime's work on the conifers came into the production phase. I had known Chris for 50 years, initially as a student of horticulture at RBG Edinburgh, where he lectured us on conifers of the world. This led eventually in 1991 to him appointing me to lead his great brainchild, the International Conifer Conservation Programme. Everyone who came into contact with Chris recognised him as a very kind and ebullient person who was always keen to share his vast knowledge about trees and ferns in a very enthusiastic manner. When I was asked by Cambridge University Press to provide editorial advice on these two monumental volumes, I had no hesitation in agreeing to help. My contribution has been merely to fill in some gaps and in no way have I attempted to make any fundamental changes to Chris's original text.

Martin Gardner
Royal Botanic Garden Edinburgh
August 2023

Cambridge University Press and the author's wife Clare Page would like to extend their sincere gratitude to Martin Gardner for his generous assistance in bringing this work to publication following Dr Page's death. He has provided invaluable help throughout copy-editing and proofing of this large project in order to make it as accurate as possible without being able to reconfirm the author's original intentions.

Structure of the Volumes

This project presents a comprehensive series of chapters, between them dealing with the evolution of the whole of the arborescent gymnosperms. This embraces all of the living woody genera of the gymnosperms, and excludes only the Cycadophyta and Gnetophyta, which are not woody, and upon which other studies exist. It thus enlarges on all of the genera of the former. Due to the in-depth nature and volume of the information presented, the whole work is presented in two successive volumes with each genus presented in a separate chapter within Part III and treated in taxonomic order, using the new taxonomic hierarchy developed by the author. Although there are exceptions, it will be clear that use of this taxonomic order also splits the genera encompassed along geographic lines. Families and genera in Part III of Volume 1 are mainly those with a predominantly wide Northern Hemisphere range focus, while those in Part III of Volume 2 have a predominantly circum-Pacific, tropical montane to Southern Hemisphere range focus. Together, the two volumes constitute a comprehensive, baseline reference with global coverage.

In order to make the two volumes as self-contained as possible, such that they can be used individually or as a pair, both include two identical introductory Parts (I and II) on *Aims, Approaches and Diversity* and *Phylogenetic Bases and Revised Taxonomic Structure*, which present a background to the overall generic presentations that follow. Part I summarises the aims, approaches, scope and objectives of the book, and presents the materials and derivations that have gone into its compilation. Part II explains the importance of taxonomic views assembled from aggregated phylogenetic information, and presents a new taxonomic structure within which all subsequent order, family and genera are then placed and discussed in an evolutionary context. Each volume also includes an identical Part IV, *From Ecosystem Services to Conservation and Sustainability*, which assembles key information from all the preceding chapters to highlight the important role of these trees in the environment. This concluding part also emphasises the need for conservation efforts informed by the strong scientific evidence presented within the volumes. Emphasis is placed on a two-horned approach involving urgent improvements in maintaining the forests and intact forest ecosystems that exist, as well as re-establishing new forest vegetation with species native to the regions, which are already closely adapted.

Within each genus chapter, more established knowledge (Sections 1–6) is presented against a white background, while the author's more recent contributions to the subject (Sections 7–10 of each genus) are identified in light grey-tinted sections. Each genus chapter contains a list of references cited in that chapter, while both volumes also contain an identical bibliography of more general references relating to the arborescent gymnosperms.

Taxonomic coverage of Volume 1	
Order GINKGOALES	Family GINKGOACEAE
Order PINALES	Family PINACEAE
	Family LARICACEAE
	Family ABIETACEAE
	Family CEDRACEAE
Order TAXALES	Family TAXACEAE
	Family CEPHALOTAXACEAE
Order SCIADOPITYALES	Family SCIADOPITYACEAE
Order CUPRESSALES	Family CUPRESSACEAE

Taxonomic coverage of Volume 2	
Order CUPRESSALES	Family FITZROYACEAE
	Family TAXODIACEAE
	Family SEQUOIACEAE
	Family CUNNINGHAMIACEAE
	Family ATHROTAXACEAE
Order ARAUCARIALES	Family ARAUCARIACEAE
	Family AGATHACEAE
Order PODOCARPALES	Family PODOCARPACEAE
	Family DACRYDIACEAE
	Family PRUMNOPITYACEAE
	Family MICROCACHRYDACEAE
	Family PHYLLOCLADACEAE
	Family SAXEGOTHEACEAE
	Family LEPIDOTHAMNACEAE

A Note About the Illustrations

The multifold purpose of the illustrations is to:

- be complementary to the textual descriptions;
- present the diversity of detailed structures present across the arborescent gymnosperms, as seen through a wide range of viewpoints and perspectives;
- illustrate the strong multidimensionality of intrinsic form of features revealed, especially when seen through multiple levels and scales;
- encapsulate characteristics of developmental stages occurring through space and time;
- capture perspectives of arborescent gymnosperm structure acquired first-hand, which are seldom scientifically depicted;
- embrace the study appeal of presentations which are otherwise so easily dismissed as uniform and uninteresting; and
- appreciate features which are of distant palaeo origin through deep time, and hence provide detail of ancient diversity which has so long existed on this planet.

All photographs are directly by the author, as sought and experienced from taxonomically authenticated, self-gathered, fresh living plant materials throughout, with the exception of 19f and 46j, which are reproduced by licence from Getty Images.