Part I Aims, Approaches and Diversity

All research begins by analysis of nature.
Michelangelo, artist and observer (1475–1564)

Look deep into nature and then you will understand everything better.
Albert Einstein, mathematician, inventor and philosopher (1879–1955)

Speak only if it improves upon the silence.
Mahatma Gandhi, observer and philosopher (1869–1948).

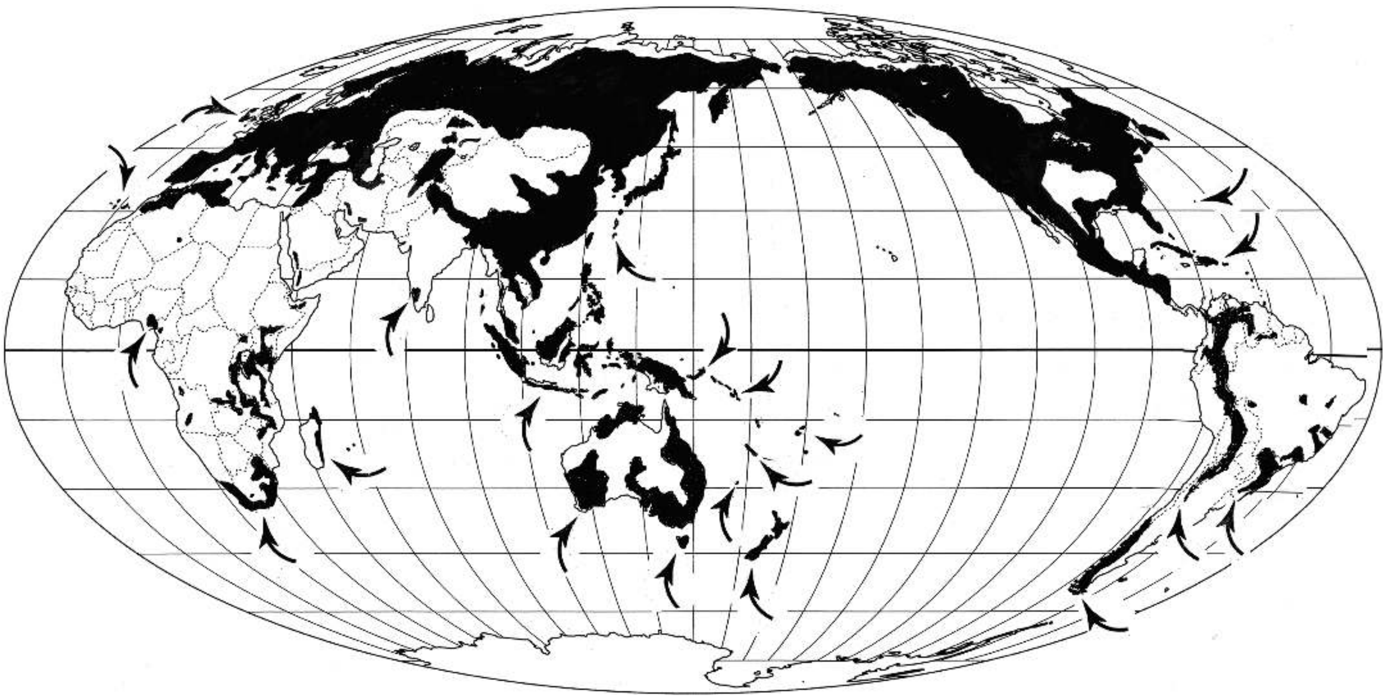
Introduction

The arborescent gymnosperms are effectively all trees globally that are not angiosperms. They are predominantly woody and resinous trees with largely narrow (often needle-like) perennial leaves, and their mostly evergreen habits contribute year-round functional potentials. Their occurrence is geographically and ecologically wide. They form the dominant trees and keystone elements of one-third of the world's forests, and are present especially through moist more-temperate latitudes of both hemispheres, as well as across many mountain ranges, including those of the tropics. These trees thus contribute substantially to the environments and sustainability of major land areas. Many have also had particularly long evolutionary histories. They collectively have formed the dominant forests of the Earth for at least five times longer than the angiosperms have existed. Their contribution to the stability of the terrestrial environments of this planet, and their recovery from extremes, have been far-reaching and extensive, and they have great potential in these respects both today and in the future.

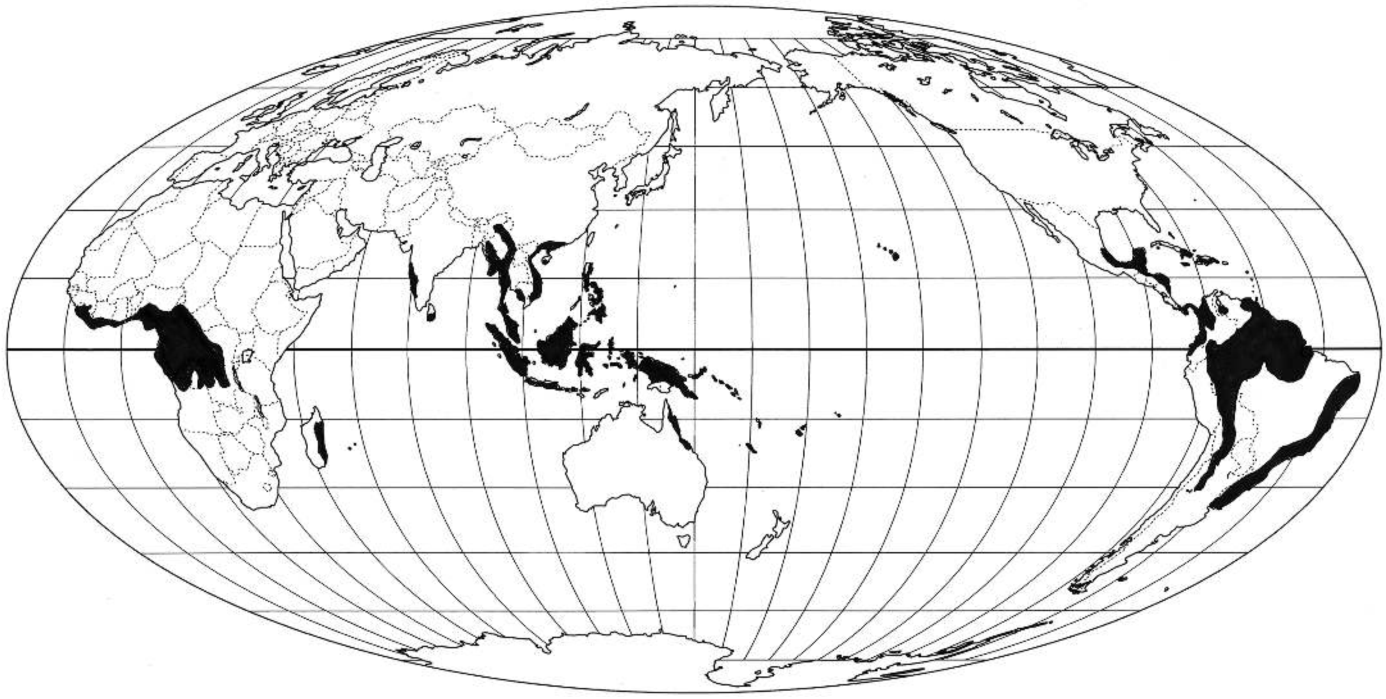
Many of the Northern Hemisphere members produce their seed in cones, but this is not true especially of many Southern Hemisphere representatives, whose seed is more often produced in association with fleshy, berry-like structures, of a great range of detailed form and derivation. Although the group have so often been overall called 'conifers', such a term closely applies to mainly modern Northern Hemisphere representatives, and especially the Pinales, to which I largely restrict it here. I have therefore instead sought an informal replacement term that is more widely applicable across both hemispheres. For this, I have adopted have and utilised the new term the 'resinifera', referring to the fact that virtually all, whether cone-bearing or berry-fruited, are united by being trees which throughout all parts are characterised by production of resin.

More technically the total ancient plant lineage of the gymnosperms is overall composed of four different groupings: the Cycadophyta, the Gnetophyta, the Ginkgophyta and the Pinophyta. Of these, the class Pinophyta is by far the largest today, containing 72 living genera and more than 700 species. Further, only the Ginkgophyta and the Pinophyta regularly form woody trees reaching tall, arborescent form, and are hence the focus of this book. This has almost certainly been true also for these two major groupings throughout the fossil record (when the Ginkgophyta have also been much more abundant and diverse). Consequently, the surviving array of these trees shows great variety in history, ecology, structural details, environmental function, vegetation achievement and strong global climatic and ecosystem-service output, applications and potentials.

Upon this basis, the research approach taken here is that study of the living members of the resinifera forms an especially valuable basis for gaining wider understanding of their functional role through their long evolutionary past, as well as providing a sound structural and practical basis in management for a sustainable future. Each genus of these trees is thus studied and analysed here in practical detail for their distinctions, diversity, distributions, ecologies, biological, adaptive and functional significances, forest contributions, environmental interactions and evolutionary achievements. Such a work is necessarily of considerable magnitude in both breadth and depth through space and time. Perhaps for this reason, there has never been any previous comparable generically led comprehensive treatise on their overall evolution, gathering data from detailed surveys of their comprehensive diversity,



Map 1 Global distribution of forests dominated by modern arborescent gymnosperm trees, presented throughout these accounts (original).



Map 2 Global distribution of modern tropical rainforests (assembled and redrawn after Whitmore 1987, included here for comparison).

setting this around fresh evidence of their living systems and developing from this analyses of the biogeodynamics of all living genera. This thus embraces the total diversity of their living systems, individualities, pathways progressed, practical and functional contributions made, phytogeographic consequences and evolutionary achievements, all of which this book seeks to uniquely uncover, assemble and integrate.

Aims and Objectives

Here we attempt to do the following:

1. Stress the importance of an ecological–evolutionary focus upon arborescent gymnosperm diversity through drawing together a powerful triumvirate assembly (see below) of independent evidence bases.

2. Focus on gaining additional novel data input from living systems, spanning all known genera, and stressing not only similarities but especially distinctions, differences and individuality of adaptations, achievement and diversity.
3. Amplify evidence of especially rarer and lesser-known genera, hitherto most often overlooked.
4. Embrace all habitats and locations where arborescent gymnosperms are present, gaining especially balances between the Northern and the often more neglected Southern Hemisphere.
5. Analyse the consequent global presence of all of these genera and their individual suites of features, development, divergences, adaptations, specialisations and long-term environmental and interactive functioning.
6. Investigate especially resulting ecological roles of their living systems, and how the dynamics of these provide vital balance to the overall vegetation and diversity of ecological–evolutionary achievement.
7. Demonstrate how phytogeographic patterns often especially link to wider environmental–evolutionary stimuli of climates, geology and events of global Earth systems dynamics, with implications for geological applications.
8. Present analyses of each genus in a comprehensive and ideas-rich, but also accessible and user-friendly, format in which small 'bites' of individual generic essays can be found and accessed in whole or part as needed.

The book strives to combine the total of these approaches, building around the author's own plant and living systems observations, novel data-source analyses and inputs gained across 50+ years. Generic entries also include fully comprehensive world geographic-distribution maps, and a strong photographic back-up to further amplify visualisation of material dimensionality, diversity and structure.

The objectives are to provide a series of comparative generic essays encompassing the great array of topics around these globally critical ancient living plants, spanning their individual biology, living functions achieved, ecosystem services provided and environmental balances commanded, as the bases for showing the global gain in their present and future onward management and sustainability.

Data Input: A Triumvirate Approach

Three main essential sources of information are thus overall surveyed, with much of that of the last added here from first-hand experience:

1. **Phylogenetic data.** This essential basis spans from molecular to non-molecular data to provide a background of comparative phylogenetic interrelationships through all taxonomic levels. While molecular evidence within this sector has achieved several vitally important sample comparative surveys, it does not necessarily replace – but rather combines with – all other (especially cytogenetic and morphological) evidence, including that available from other structural and developmental (e.g. embryological) sources. The bases of these different sources add to and widen the perspectives of each other. Indeed, data from cytogenetics yields awareness especially of vital other factors occurring, such as processes of hybridisation and occasional polyploidy emerging, which have been interpreted here to have contributed substantially to achievement of locally – and perhaps more widely – far greater phylogenetic complexity than previously appreciated. From this aggregate, more objectively balanced phylogenetic assemblies supporting broad global evolutionary overviews are constructed. Especially highlighted throughout is information on the depths of separation between the taxa in question. The vitally important frameworks derived are then built towards understanding evolutionary distances, divergences, progressions achieved and perhaps the steps and pathways involved.

   I have used phylogenetic data especially widely throughout this book to create a relative sequence of successive placement of the taxa (here especially genera) presented and discussed. The relativities established by this phylogenetic information have thus resulted in construction of a solid and consistent uniform new taxonomic background throughout, with construction and hierarchical placement of all classes, orders, families and genera across the whole arborescent gymnosperms revised. This forms the basis of their presentation throughout.
2. **Palaeobotanic data.** Because they have very many hard parts, the arborescent gymnosperms often tend to fossilise well, and always have. Their many hard parts (leaves, twigs, cones, bark, wood and even resins) have enabled individual trees to leave strong fossil signals in the palaeobotanic land-plant record. Close study of such ancient elements of the Earth's forests through time thus offers a long-accumulated perspective of these dominant forest-forming arborescent gymnosperms as multiple 'windows on the past'. This shows the living members to often have withstood many changes during Earth's history, and the trees themselves thus harbour experience of resilience to eons of evolution in their unique gene arrays. We thus have an extraordinarily strong palaeobotanic basis from which we can build pictures of past occurrence with strong confidence, offering often vital long-term bio-indicator values of global terrestrial times and environments of the past. Significantly, too, important areas – some now without tree growth, such as Antarctica – are recorded with respect to former palaeo-contrasts, with forest presence. In all areas, additional new materials continue to be actively produced, adding often fresh detail of patterns of evolutionary specialisation. Where appropriate, these are set against backgrounds of regional information of known geological histories and influences of Earth systems dynamics in space and time.

   Palaeobotanic data, to me, also helps to show the presence of other past taxa that have existed but become subsequently extinct, but which may have nevertheless contributed to palaeo-phylogenies and perhaps even to at least some still-living genomes. For each genus separately within this book, I have thus assembled the known palaeobotanic (fossil) data directly from numerous independent sources, gathered here on a global through-time basis for each genus for the first time. It spans survey of variations in successive plant structures, living systems, palaeo-diversity, space–time progressions, related groupings, diversification and extinction events, evolutionary pulses and stases, palaeo-abundances, paleo-ranges, linked possible palaeoclimatic ecological settings and known habitats.

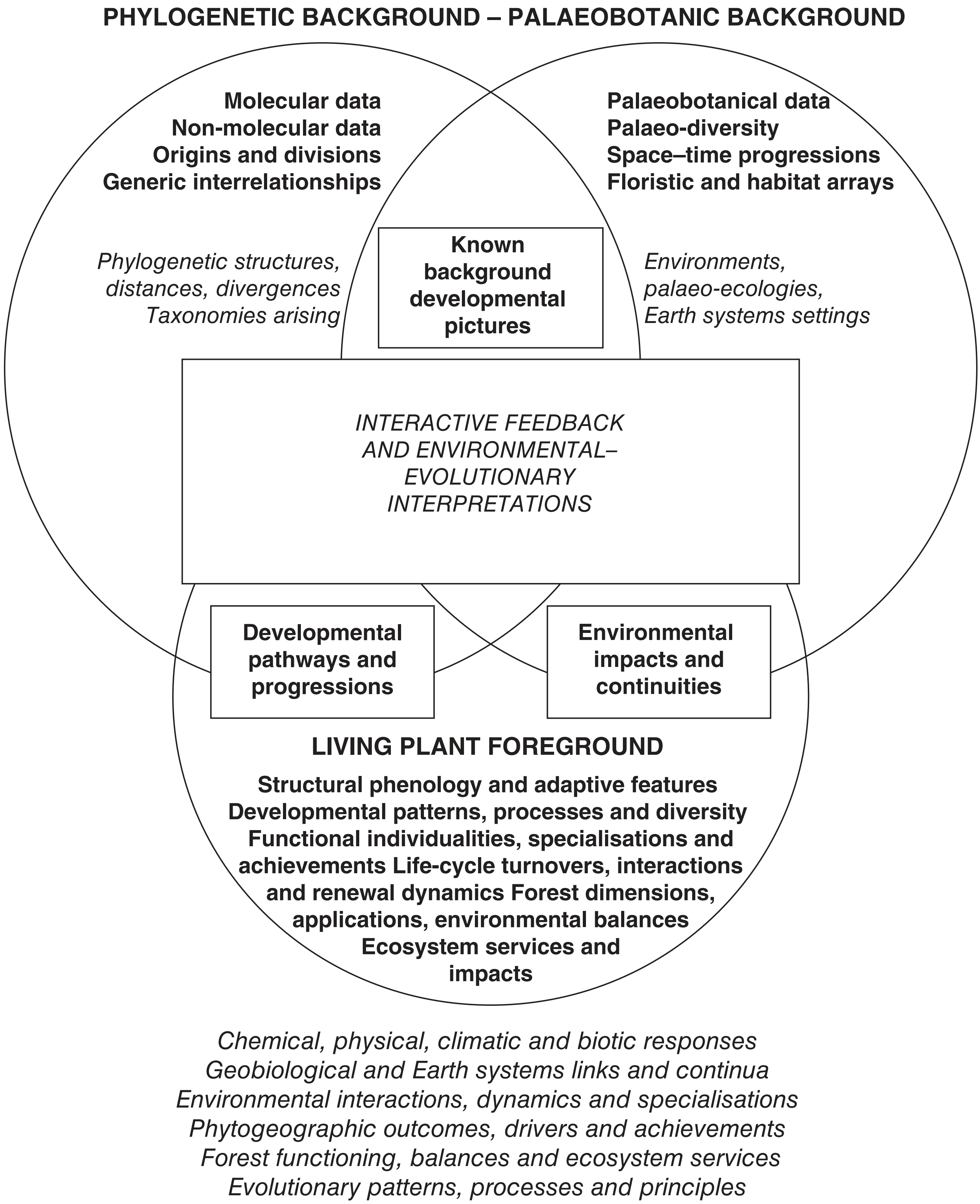
I have used palaeobotanic data as individual major early-case information for each genus, to form a background of what is currently independently known of the past presence of each genus, the timescales involves and geographic locations of fossil finds. I have also included with it any discursive information, such as ideas regarding structural differences and similarities, diversities and past communities, habitats and environments in which each genus has occurred, as far as direct fossil evidence has succeeded in contributing to these.

3. **Living systems data.** This main aspect throughout forms the *foreground* of evolutionary studies covered here. Such material has the advantage of having a wide taxonomic sweep reflecting the fullest expression of generic make-up, diversity and taxonomic authenticity. It also displays structure and phenology, adaptive features and variations. Evidence of the significance of adaptations and diversities of structures are sought throughout, and an additional strength is that all can be further checked through sensitive combinations of repeat observation, experiment and feedback. Close observations are possible through a wide range of scales. Here we present detail at levels never before attempted, geographically, ecologically and experimentally widely, across time, and structured to be complementary and comparable across the whole array of living genera presented on a global scale. The book attempts to include within this, as far as possible, details of patterns and processes of growth and development, life cycle progressions and turnovers, forest structures formed, ranges and habitats occupied and environmental interactions and influences in both space and time, and to draw from these dynamic evolutionary perspectives. Detailed functioning of trees and whole-forest living plant ecosystems, and the intricacies involved, are followed across broad taxonomic spectra, offering insights about how features offer opportunities to appreciate their roles as functional elements of ecosystem behavioural dynamics. As well as clear, larger-scale processes, evidence of accumulations of many small-scale processes become evident, occurring in intimate and scattered episodes and mosaics. Vital attention is given to how trees interface and interact with the many aspects of environmental processes about them, and I have sought to especially display diversity of form, distinctiveness of functionality and individuality of evolutionary achievement. It is held that all of these, as seen today, have also contributed to moulding the pathways of individual generic evolution through often long periods of evolutionary time. Considerations derived from the breadth and depth of such plant living systems data lead especially to important perceptions of the biological complexities so often involved in their continuity and the evolutionary processes involved.

I have used living systems data as the core of this book. The book contains many additional new contributions from first-hand experience. From these it can be seen that because most of the living members are essentially survivors of often long periods of evolutionary time, there are vast sources of information locked-up within the structures and dynamics of these living plants and their systems relevant to long periods of Earth history. Much of this, in relation especially to functions, processes, ecologies and environmental interactions, is explorable and determinable. The book thus provides a broad, in-depth, recordable, ecodynamic and environmentally interactive study, with many principles and long-term implications as a result. In terms of the breadth of this data, in an important brief history of the whole of gymnosperm diversity through time, Anderson et al. (2007) estimated that across the span of 375 million years of gymnosperm presence on Earth, there have been a total of 10 classes, 37 orders and 84 families of these plants. A majority of these have likely been arborescent, and their contribution to the vegetation of this planet and its functioning has thus been immense. Of the living members that still form trees (termed the 'living arborescent gymnosperms' as treated here), I recognise a total of 2 classes, 7 orders and 23 families still extant (see Part II). Thus, compared with those that have existed across geological time, those still living are only a moderate-sized sample. But, in an objective perspective, these arborescent gymnosperms are very much the equivalent of the reptiles of the animal kingdom (as much as the Pteridophyta are the Amphibia – Page 1988), and of the present survivors, very many are more exactingly the living equivalent of dinosaurs. In the arborescent gymnosperms, a large contingent thus survived the Cretaceous–Tertiary mass extinction event that killed the dinosaurs. Having a total of 2 classes, 7 orders, 23 families, 73 genera and around 700 living species of these plants, plus the whole of the ecosystems they form, still alive to study remains spectacular by any standard.

Outcomes Encapsulated

Each of the above *triumvirate* of principal resources offers independent fields of data and wider information for each of 73 genera, relevant to understanding evolution within each. These have the strength of being multiple in source and both additive and comparative in content. That of (1) provides a first background step that effectively answers basics of the 'what' of the evolutionary process of each genus; (2) provides further background steps that develop outlines of much of the 'when' and 'where'; and (3), as the living *plant systems foreground*, seeks to advance much of the 'which', 'how' and 'why', and provides visualisations of pattern and process, pathways



The *triumvirate information assembly* utilised here. Components in italics are aspects provided especially first-hand here.

and diversity, environmental links and interactions and the possible resulting principles.

There have been many opportunities to test and re-test all elements. Consequent dominantly practical, structural, developmental, dynamic and environmental analyses have thus provided multifold unique bases around which new ideas have been generated or have gradually unfolded and assembled towards collective evolutionary ideas. From these datasets, particular emphases are placed upon achieving combined-balanced perspectives of how evolution has proceeded and is still proceeding in the 'real' world, and the implications of this through a space–time perspective.

Living systems of arborescent gymnosperms are then used as the primary core of these studies, around which the data is set, because of their considerable global significance in several important respects:

- They allow the whole of averages and even extremes of structure, function, development, processes, patterns and sequences and adaptive detail to be studied in considerable whole-plant living systems contiguous detail.
- They do this from across a wide range of phylogenetic, taxonomic and life form spectra of living members, between them showing virtually all conditions of form present, in scales from the microscopic to forest trees.
- They allow records of sequences and succession of materials through all life stages of individuals to be analysed.
- They open the opportunity for widespread sampling from across geographic ranges, demonstrating full ranges of ecologies and tolerances.
- In studies of the living systems they allow all variations of interactions of the living members with their full diversity of ecosystems and environments to be formed.
- Through this route, pictures of evolutionary progression thus build, pointing towards principles, strategies and environmental links today, and also likely those through long periods of Earth evolutionary history.
- The dynamics arising also indicate fuller pictures of likely interactions of plant families and genera with wild environments through the course of their evolution.
- They can demonstrate how these trees, as integral components of globally forested environments, support ecosystem services.

Using the living plants and their systems as a central core thus provides a strong, central 'Rosetta Stone' around which information from all other resources can be best assembled, displayed, interrelated, analysed and interpreted. I also bear strongly in mind where there may be gaps. For example, while the fossil record shows many genera which are no longer extant to have existed, which were once living plants too, others may have also existed (especially, for example, in locations that may have left no fossiliferous trail). On the other hand, the living plants can show the presence of some individual genera (e.g. *Parasitaxus*) that are as-yet unknown from the fossil record, even as a life form. They also show, often in detail, how life cycle turnovers take place.

In presenting the dynamics of the whole of this data, I have throughout also used the terms 'pattern' and 'process' which mark, for me, a particularly strongly recurring theme of environmental–evolutionary developments and impacts that are present through wide phylogenetic spectra. 'Pattern' occurs in a morphological sense from micro-structures to whole trees, through an enormous range of scales, and both in structure and ecology. 'Process' especially reflects ways in which features of living plants build, interact and effect functioning and progression of taxa, from the structural development and life cycles of individual plants to the many further dynamics of whole-forest structures and ecosystems, their occurrence, recurrence and progression through time. Together, developments balancing and rebalancing in time and scale are established, and the resulting forest structures can be mosaic-like in complexity and ever-changing in dimensions and time. *Evolution of the Arborescent Gymnosperms* thence derives from the total of these data inputs and considerations. It shows clearly deep diversity derived through time, and upon this, strong individuality of adaptive solutions, environmental interactions and evolutionary experimentation, differing directions pursued, selections, successes and extinction failures, developmental potentials arising and renewing from diverse stocks, and the drivers and dynamics of all of these.

All have been constantly subject to differing geoenvironmental opportunities presented by the very functioning of the planet upon which they occur, and the many changes and challenges of Earth systems dynamics. Evolutionary individuality of separate genera is what I seek to especially emphasise, from which many principles arise. It is this strong individuality that demonstrates the distinctiveness of their many diverse evolutionary achievements and pathways scribed. 'Diversity' (*sensu* Page 1979) is, then, the core of what has been gained, inherited and achieved, at any point, and 'interactivity', 'complexity' and 'flexibility' all underlie the abiding evolutionary potentials that are continuously apparent.

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Part I Phylogenetic Bases and Revised Taxonomic Structure

I have called the principle, by which each slight variation, if useful, is preserved, by the term Natural Selection.
Charles Darwin, English naturalist, observer, geologist and evolutionary visionary (1809–1882)

And that sense of hierarchy, of a pyramid in which layer upon layer, runs through all the ways that we look at nature. . .
Jacob Bronowski, mathematician and philosopher (1908–1974).

The whole history of science has been the gradual realization that events do not happen in an arbitrary manner, but that they reflect a certain underlying order. . .
Stephen Hawking, theoretical physicist (1942–2018)

Placement of Overall Living Gymnosperms and Phylogenetic Backgrounds

Three Major Land-Plant Groups Compared

Three major land-plant groups, widely recognised as the Pteridophyta (informally 'pteridophytes'), Gymnospermae (informally 'gymnosperms') and Angiospermae (informally 'angiosperms') together form the living *vascular plants*. Together these compose the dominant vegetation of all landmasses of the Earth. Gymnosperms differ from pteridophytes (ferns and fern allies) in that the separate free-living gametophyte generation seen in the pteridophytes is no longer free-living in the gymnosperms. Gymnosperms share this absence of a free-living gametophyte with the angiosperms, as well as possessing the production of seeds, and thus seeds (multicelled diploid propagule components of the life cycle), not spores (single-celled haploid propagule components, as in the pteridophytes) are the main physical disseminules of both gymnosperm and angiosperm life cycles. Consequently, gymnosperms and angiosperms together collectively form the Spermatophyta in this important seed-bearing respect, but gymnosperms differ from angiosperms in always having technically naked ovules (i.e. gymnosperms as a whole are seed plants with an ovule that is not enclosed within a carpel, in contrast to angiosperms). The seeds of gymnosperms are thus directly exposed to the atmosphere at least when the stage of pollination is reached, and may remain exposed or become partly externally protected through subsequent stages of ovular development, or remain naked throughout.

Trends of Overall Evolutionary Structural Progression

The evolutionary surveys achieved here show the principles of development, often forming repeating progressions of pattern and progress through numerous arborescent gymnosperm subgroups. A thesis for overall structural progressions developed through these generic studies is that overall evolutionary trends have generally progressed in the direction of from earliest simplicity to fairly early complexity through simple initial repetition of successive similar structures. This has then typically been followed, often through further long-term evolutionary progression, towards often progressive simplification, associated with increasing specialisation of unitary functioning and individualisation of structural complexity with detailed adaptive significance. These processes all build to increasing evolutionary complexity, and it is the outcomes of accumulations of such events that taxonomic structures derived from the living plant outcomes then attempt to reflect.

Taxonomic aspects aim to accord with phylogenetic ones, with usually more simplified – but comparatively accurate – structure. Taxonomy thus takes such more widely considered information and accommodates it into a resulting reasoned array, giving relativities of divergences weight through hierarchical structure. All biota, as taxonomic elements ('taxon/taxa') through all ranks are given names by which each can be identified as the accepted reference to that particular element, across all disciplines to which it may apply, and established in the light of all information available. Within this structure, taxonomy seeks to offer descriptions, involving especially 'key' data by which each unit is identifiable and can be discretely encapsulated. A good taxonomic presentation is hence analogous to a map of a complex underground railway system – it serves to enable the user to find their way around within an acceptably stylised system which is itself faithful to reality. But it incorporates simplified directions, placements and locational relativities of all hierarchical categories and the names of the main and smaller stations within realistic practical frameworks.

Overall taxonomic structures are also usually built, in the first place, around evidence from living plant systems as the materials of these are in a unique position to provide the necessary detailed structural arrays by which each plant part can be unambiguously known, and states of organic connectivity can be unambiguously sampled. This allows the necessary structural observations to be established for the taxonomic structures devised. Large-scale sampling can be completed, and development and variation witnessed. Importantly, this does not mean that structures or additions cannot be further added or modified with time, especially as new discoveries may be made. Fossil materials can be attached to these taxonomies, adapting and adding to them as appropriate.

In assembling views of the taxonomy of this major living plant group, full knowledge of their phylogenetic background is thus essential. For such phylogenetic backgrounds, the sum of all known events and pathways provides a collected assembly of evidence available, spanning not just well-selected molecular analyses, but also especially morphological, developmental, life cycle progressions, cytogenetic, palaeobotanic evidence and understandings of adaptive specialisations in relation to environments. This information thus builds independently supported frameworks from which to begin to assemble our best outlines towards understanding phylogenetic backgrounds.

Especially significantly emerging from modern molecular studies is that in the gymnosperms particularly, although the whole group is shown to be essentially monophyletic in its initial origins, very early divisions gave rise to the beginnings (divergences) of several separate but long-standing basic stocks. These, in due course, gave rise to modern classes, orders, families and genera. Such evidence shows especially that nearly always these divergences are older, sometimes far older, than previously understood, and these perspectives have shown how ancient the arborescent gymnosperm separations are, and hence increased the understanding of the depths of divisions within the living member groupings. These perspective are now incorporated in setting the framework of the taxonomic structure of the arborescent gymnosperms proposed here.

Building from this background, the total collected data has shown how the subsequent progression of evolution has been both highly complex and manifestly multidimensional in both space and time. Thus, its scientific study must be approached with due caution. It must always be borne in mind, for example, when interpreting molecular cladograms, that these tend to show only what is known from narrow living sample bases, and only in two dimensions. My philosophy in approaching this topic is that presentations that necessarily accept the dogma that cladistic information is the whole picture can thus be misleading, or, at least, only a partial sketch of potential actualities. In probably all groups there have also been many other variations and events, many little, if at all, known, such as the presence and extinction of members, which have themselves also contributed to the long-term actualities of the evolutionary process.

A further evolutionary caution of mine is that not all evolutionary pathways have necessarily been divergences, as virtually all cladograms tend to presume they can only be. In my book there have also been various additional patterns, including parallelisms and especially convergences. These include adaptive development in increasingly close parallel under similar environments, representing further 'comings together' in the form of interspecific (and sometimes even intergeneric) hybridisations and even complete introgressions and processes of polyploidy. These then become the basis of further selection and reselection from appropriate successful progeny, leading to long-term survivorship of some. The occurrence of such events now seems to be beginning to become independently confirmed by new closely focused molecular techniques applied to increasingly detailed, well field-sampled arrays, showing that multiple processes of evolutionary dynamics may have been involved in both space and time.

Support for Major Subdivisions within the Overall Gymnosperms

Many aspects of study of gymnosperm interrelationships have been expanded in an array of publications. These reflect an increasing knowledge base, especially on morphological and developmental grounds, through time. In parallel, a wide variety of interrelated research approaches have each also contributed to growing understanding of relationships among extinct and living families. Backgrounds are also strong in drawing parallels and comparing broad adaptive, developmental, phylogenetic or evolutionary perspectives between these and other ancient major plant groups. Outcomes demonstrate that the gymnosperms stand strongly apart from the origin of the angiosperms as well as the pteridophytes, and that within them the resinifera have achieved extraordinary modern diversity of each of form, structure, ecological habits, adaptive potentials and environmental interrelationships.

In addition, modern increasing largely molecularly derived evidence, which includes evidence of rearrangements that alter gene order, intron gains and losses and whole-gene losses, and relativities of divergences, has come increasingly to the fore. These largely independent molecular bases can especially reflect additional detail of the ancientness of various phyletic links and the depths of divisions which separate them. Data overall indicate that many major groupings tend to have ancient origins, of which especially the molecular data can provide a 'Rosetta Stone' in establishing relativities of placement of critical groupings, effectively established long evolutionary distances and substantial divergence relativities and their likely sequencing and time estimates between major groups.

Using the provisional molecular nomenclature as originally outlined by Chaw et al. (1997), the main molecular groupings have been widely recognised as *Gymnosperms A* + *Gymnosperms B* + *Gymnosperms C* :

- *Gymnosperms A* constitutes the first of the three major gymnosperm groupings. It contains Cycadales plus Ginkgoales, which together first form a clade that is sister to all remaining extant gymnosperms (Chaw et al. 1997). This cycad–ginkgoalean clade thus forms the earliest components of the gymnosperm lineage. Within this major gymnosperm assembly there is an early dichotomy into the cycadalean and ginkgoalean lines. The Cycads thus form a non-arboreal (or sometimes just sub-arboreal) component of Gymnosperms A, and the Ginkgoales, and hence the single living arborescent genus *Ginkgo*, its sole truly *arborescent* surviving member.
- *Gymnosperms B* constitutes the second of the three major gymnosperm groupings, sometimes referred to as 'conifers I'. Although relationships of Gnetales remain somewhat unsettled, a particularly significant and consequential molecular-based finding is that there is an evolutionary split of Pinaceae from other conifers (Chaw et al. 1997). As a consequence, there is growing support that *Gymnosperms B* constitute a second major gymnosperm grouping. Here, a pinalean line (recognised here as the living subclass Pinideae) themselves form a distinctive monophyletic group within this single *Gymnosperms B* collective clade (Doyle 1996; Chaw et al. 1997). Under these interpretations, the pinalean conifers are thus the only surviving arborescent members of a former 'Gnetales–Pinales' clade, while the non-arboreal components, *Ephedra*, *Welwitschia* and *Gnetum*, are themselves regarded the 'relictual extant remnants' of a group of plants that were once widespread and much more diverse. Indeed, both affinities and depths of divisions attest to the age of *Gymnosperms B* as a whole. However, within the Pinales, many living members show a wide range of features which collectively combine ancientness with potentials in which some genera continue to show considerable diversification today (e.g. Page 1990; Farjon & Page 1999; Eckenwalder 2009; Farjon 2010). So structured, the pinalean conifers are also the grouping which in practice accommodates most of the major arborescent gymnosperm genera and families that produce large and usually long-lived woody cones, as these are already widely established and recognised in a popular sense.
- *Gymnosperms C* constitutes the third of the three major gymnosperm groupings. Here there is increasing support for the view that this group embraces the remainder of plants formerly widely grouped collectively as 'conifers' (Doyle 1996; Chaw et al. 1997), and thus sometimes referred to as 'conifers II'. Within this assemblage, three further monophyletic clades have been further recognised, which, according to Chaw et al. (1997), include Phyllocladaceae–Podocarpaceae, Araucariaceae and Sciadopityaceae–Taxaceae–Cephalotaxaceae, Cunninghamiaceae and Cunninghamiaceae, Cupressaceae and Taxodiaceae, as formerly recognised. It thus seems likely that *Gymnosperms C* are also an extremely ancient assemblage with high past diversity. Of these, the extant members are only some of the survivors, but even these clearly show a wide range of features that collectively combine ancientness with potentials in which some of their families and genera continue to show considerable diversification, actively continuing to this day (e.g. Page 1990; Farjon & Page 1999; Eckenwalder 2009; Farjon 2010). Since a very great majority of members, and often all, of each family and most genera represented among survivors of *Gymnosperms C* are woody tree-forming plants, there is a strong phylogenetic coherence.

Taxonomic Impact

It is thus clear that the woody tree-forming (arborescent) members of the gymnosperms (the arborescent gymnosperms), with which this book is concerned are thus an eclectic group. Today, they do not fall exclusively into either Gymnosperms A, B or C, but instead at least some clearly arborescent members are present in each of these major groupings, and these divergences are themselves old. These clades represent early, deep, ancient divisions, which have existed through much of the fossil history of the whole of the gymnosperms, and provide a multilayered strength to the establishment of a new overall taxonomy. To accommodate this, the here-proposed updated taxonomy thus includes substantial upward nomenclatural decompression, itself establishing many proposed higher rankings. Major derivations from the above phylogenetic data are hence as follows:

1. The only surviving arborescent generic member of Gymnosperms A is accordingly included under the taxonomic declensions of class Ginkgophyta (established on the original basionym of *Ginkgo* Linnaeus, Mant. Pl. Altera: 313 [1771]). Class Ginkgophyta contains subclass Ginkgoideae as the only living subclass, and the single living order Ginkgoales. This taxonomic order then contains a single family Ginkgoaceae. Nomenclatural usage of this grouping derives from the existing accepted Linnean basionym for family Ginkgoaceae, which consequently still exists and is available for use.
2. The surviving arborescent generic members of the molecularly recognised Gymnosperms B are accordingly here included under these taxonomic declensions as class Pinophyta, subclass Pinidae as the only living subclass, and the single living order Pinales. This order then contains all

of the existing genera, which now have space to be grouped into four families (one of which is family Pinaceae). Nomenclature of this grouping is based on the existing accepted basionyms: class Pinophyta established on the original basionym of *Pinus* Linnaeus, Sp. Pl. 1000 (1753), that of subclass Pinidae following its usage by Cronquist, Takhtajan & Zimmerman, Taxon 15:134 (1966), endorsed also by the present author. Subclass Pinidae (establishing the term of informal reference of the resinifera, to this part especially retaining and now restricting the informal term 'conifers') thus includes the single living order Pinales.

3. The many surviving arborescent generic members of the molecularly recognised Gymnosperms B are accordingly included under these new taxonomic declensions as class Pinophyta, subclass Taxidae. Class Pinophyta, subclass Taxidae, the only living subclass, contains a further five successive living taxonomic orders: order Taxales, order Sciadopityales, order Cupressales, order Araucariales and order Podocarpales. These orders then contain, between them, a total of 16 here-revised living family structures, some containing further subfamily declensions. (The nomenclature of subclass Taxidiae is established on the original basionym of *Taxus* Linnaeus, Gen. Pl. 312. [1737], and follows the proposed basionym of subclass Taxidae by Ehrendorfer ex Reveal, Phytologia 79:71 [1996]).

Proposed Fully Revised New Taxonomic Overview

Taxonomic Assembly Process: Vertical Decompression

This book, through developing extensively updated evolutionary perspectives which accord with revised phylogenetic frameworks, demonstrates the consequent strong desirability of supporting these studies with an updated, well-integrated revised taxonomic framework for the whole of the arborescent gymnosperms. Such has thus been assembled here. A strong driver has also been, importantly, decompressing what I have seen as existing degrees of over-compression of most existing lowermost categories in earlier gymnosperm taxonomy. Through this process, I have thus effectively extensively upgraded especially many higher-category levels. This is done wherever possible retaining existing well-known terminology roots, so that the overall resulting structure has itself evolved, rather than started anew.

SUBKINGDOM SPERMATOPHYTA (SEED PLANTS)
PHYLUM GYMNOSPERMAE

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[THE 'NON-ARBORESCENT GYMNOSPERMS']
(not treated further within this book)

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Class: CYCADOPHYTA
  Subclass: Cycadae
    Order: CYCADALES
      Family: CYCADACEAE (CLASS AND ORDINAL TYPE)
      Family: ZAMIACEAE
Class: GNETOPHYTA
  Subclass: Gnetidae
    Order: GNETALES
      Family: GNETACEAE (CLASS AND ORDINAL TYPE)
    Order: WELWITSCHIALES
      Family: WELWITSCHIACEAE
    Order: EPHEDRALES
      Family: EPHEDRACEAE

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[THE 'ARBORESCENT GYMNOSPERMS' (RESINIFERA)]
All as treated fully within this book.

Class: GINKGOPHYTA
  Subclass: Ginkgoidae
    Order: GINKGOALES
      Family: GINKGOACEAE (ORDINAL TYPE)
        01. Ginkgo L.

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Class: PINOPHYTA
  Subclass: Pinidae
    Order: PINALES
      Family PINACEAE (ORDINAL TYPE)
        02. Picea A. Dietr.
        03. Cathaya Chun & Kuang
        04. Pinus L.
      Family LARICACEAE
        05. Larix Mill.
        06. Pseudotsuga Carrière
      Family ABIETACEAE
        07. Abies Mill.
        08. Nothotsuga Hu ex C. N. Page
        09. Tsuga Carrière (inc. *Hesperopeuce* Lemmon)
        10. Keteleeria Carrière
      Family CEDRACEAE
        11. Pseudolarix Gordon & Glend
        12. Cedrus Trew

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  Subclass: Taxidae
    Order: TAXALES
      Family TAXACEAE (ORDINAL TYPE)
        13. Taxus L.
        14. Pseudotaxus W.C. Cheng
        15. Austrotaxus Compton