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Conifers of the World

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Summary. When a natural group of plants has over many years been comprehensively and intensively studied, a large body of data, analysis and evaluation has accumulated. It is in the nature of such work on the taxonomy of such a group that this information is to be found scattered in various publications, such as research papers, checklists, monographs, Floras and other compilations. As time and research progress, some of this information will become outdated and superseded by new publications, but other information remains current and valuable. To give a review of this can provide us not only with a guide to this resource, but also with an introduction to the group in question. It may stimulate new research, as inevitably we will find that all has not been said and done, even about a group so well studied as the conifers. I hope that this paper will meet these aims.

Key Words. Coniferae, conservation, ecology, economic importance, fossil record, phylogeny, temperate forests, tropical forest.

Introduction

To most of us who live in the temperate zone of the northern hemisphere, conifers are among the most familiar trees and indeed an everyday sight. Forests in the Boreal Climate Zone consist almost exclusively of conifers and cover vast tracts of land in North America and Eurasia. In many mountain ranges too, conifers make up the forests. But at lower latitudes, and in most of the lands in the southern hemisphere, conifers are much less conspicuous. Yet the majority of species occur there, not in the north. The island of Borneo has 39 species, the small Pacific island of New Caledonia has 43, yet in all of Europe there are only 41 species of conifers. This is the first fact that tells us that there is more to conifers than the familiar pine and spruce forests of the north. With a total of around 615 species, if they were a genus the conifers would be a large taxonomic group. But, as will be explained, we should recognise them at a much higher rank, most probably as a subclass. Then, compared with the angiosperms, or even the ferns, they become perceived as a small group. The fossil record, though fragmentary as it always is, gives us the best evidence that this diminutive size is due to extinction. But phylogeny reconstruction demonstrates that some clades now extant have radiated into substantial numbers of new species. Conifers as a whole may be a relict group of primitive seed plants, but they have been around for at least 300 million years and are

apparently still able to adapt and diversify. The classification of conifers reflects this history, encompassing both a monospecific family that can be traced back to the Jurassic and a genus of well over 100 species. They occupy all habitable continents and occur in many environments, some barely suitable for vascular plant growth. While adapting to changing environments conifers also had to find means to cope with the rise of angiosperms, which attained a species-level diversity vastly greater than the conifers ever had, even in their Mesozoic heyday.

As an ecologically conspicuous and generally useful group of woody plants, conifers have had a long history of scientific research as well as horticultural and forestry attention. As can be expected, much of this work has traditionally been centred on the conifers of the north; detailed knowledge of many of the southern, and especially of the tropical, conifers is still lacking. Genuine new species are still to be discovered there, and several have been described from scant material found in almost inaccessible localities. Unlike the northern conifers, the tropical and southern conifers do not tend to form forests or even single-species stands; they typically occur scattered among other trees or shrubs in highly diverse ecosystems. As they often have broadly flattened leaves instead of needles, conifer trees in a tropical forest can be inconspicuous. They have no true flowers that would stand out at flowering times. Yet their timber is often valuable and sought by those

who exploit the natural forests in the tropics and elsewhere.

Logging, general deforestation and other man-made threats have caused the conifers to become one of the most threatened groups of woody plants. According to the latest IUCN Red List Assessment published in 2013, 34% of all conifer species are threatened with extinction. The lower latitudes and the southern hemisphere are also the regions of the world where conifers are most often threatened. Another major extinction is likely to happen soon as a result of mankind's activities, but it is probably just one of many in the long evolutionary history of this fascinating group of plants.

History

Much has been written about conifers since the 19th century and a review of the more influential publications was given in my *Monograph of Cupressaceae and Sciadopitys* (Farjon 2005). In that review I divided this literature into two categories: conifer manuals and taxonomic works. Traditionally, the manuals, compiled as they were by Europeans, were descriptive textbooks emphasising conifers taken into cultivation in Europe. This meant that they would include 'varieties' that had their origin not in nature but in gardens (now treated as cultivars) and exclude taxa not in cultivation, mostly the tropical species. As the latter continued to be described in taxonomic journals, some manuals started to include them, but with only a cursory mention. Taxonomic works are descriptive publications that treat taxa, such as a family or genus, aiming to include all known species in the group regardless of their utility in horticulture or forestry. However, throughout the period, now approaching 200 years, not only have both categories existed side-by-side, they have also influenced each other. Cultivation enhanced an understanding of morphology that could rarely be obtained from often scant and poorly collected or preserved herbarium specimens, so that even in taxonomic works a bias towards conifers known from cultivation remained apparent. Conversely, with increasing taxonomic information, conifer manuals became more serious in their attempts to include all species and not only those in cultivation. In the English language, the earliest manual to present a more comprehensive treatment of the conifers was *A handbook of Coniferae* (Dallimore & Jackson 1923) which passed through four revised editions up to 1966. Yet it still aimed at an audience of "gardeners and foresters rather than botanists" and its popularity meant that it was almost universally regarded as the authoritative textbook on conifers long after it went out of print. In the German language, the *Handbuch der*

Nadelgehölze (Krüssmann 1972) included all known species only in its second edition of 1983; despite this it was translated into English as *Manual of Cultivated Conifers* in 1985. The only comprehensive taxonomic treatment of conifers produced in the second half of the 20th century remained Henry Gausson's complicated 15-part *Les Gymnospermes actuelles et fossiles* (Gausson 1942 – 1968). This work was largely ignored in the wider world of conifer research, mainly because of its near inaccessibility of scattered information about individual taxa, but perhaps also due to its deliberate omission of synonymy. Towards the end of the 20th century, we were still awaiting a modern, updated, comprehensive taxonomic treatment of all known conifers, without horticultural or regional bias. A first step towards this goal should be a world checklist that would review all published names of taxa and propose a workable taxonomy based on the most recent research in conifer systematics. This became my first task at the Royal Botanic Gardens, Kew and resulted in the *World Checklist and Bibliography of Conifers* (Farjon 1998; 2nd edition 2001, Fig. 1). This checklist could serve as a basis for a fully descriptive taxonomic treatment of the conifers, in which cultivation would be noted but not emphasised. In the meantime, from the mid-1980s onwards, phylogenetic analyses based on molecular data resulting from DNA sequencing began to influence and then largely determine taxonomic classifications. This change of emphasis also impacted on conifers, although for a long time such studies focused on a limited number of taxa, first in Pinaceae (especially *Pinus* L.), then Cupressaceae, and only recently other families and finally sampling all conifer families and genera. The resulting phylogenies have only partly influenced the comprehensive treatments of conifers published after 2000. This is due mainly to an acceleration of publications after 2008, of manuals and taxonomic works as well as phylogenies based on molecular data. Proposed changes in classification followed hard on the publications of these books and were sometimes in conflict with each other. The first taxonomic work to appear in modern times treating all known species of conifers was *Conifers of the World: the complete reference* (Eckenwalder 2009), shortly followed by *A Handbook of the World's Conifers* (2 volumes) (Farjon 2010; 2nd edition 2017, Fig. 1). Then came *Conifers around the World* (2 volumes) (Debreczy & Rácz 2011) which, however, only treats "conifers of the temperate zones and adjacent regions." So as not to be accused of lagging behind, the cultivated conifers received their most comprehensive treatment yet, in the form of the Royal Horticultural Society's *Encyclopedia of Conifers* (2 volumes) (Auders & Spicer 2012). This work follows

Fig. 1. A comprehensive treatment of the conifers in four volumes.

the taxonomy of Farjon (2010) for the genera and species, with all cultivars known linked to the species names. In part because Farjon's *A Handbook of the World's Conifers* lacks distribution maps, the 'companion volume' *An Atlas of the World's Conifers* (Farjon & Filer 2013, Fig. 1) was published, with maps based on herbarium collections for all taxa. In just eight years (from James Eckenwalder's book in 2009 to Aljos Farjon's second revised edition in 2017) the conifers have received their most comprehensive treatment ever.

Fossil record

There is a relatively abundant record of fossil remains of conifers, dating back to the latest stage of the Carboniferous Period (Late Pennsylvanian = Gzhelian, 299 – 303 Ma) with the fossil tree *Thucydia mahoningensis* Hernandez-Castillo, Rothwell & Mapes, discovered in the coal seams of Ohio. This small tree resembled a young, pot-grown Norfolk Island pine (*Araucaria heterophylla* (Salisb.) Franco; see Farjon 2008: 79) but its reproductive structures were very different and unlike any living conifer, both its pollen cones and seed cones were compound. It has been classified in its own (extinct) family Thucydiaceae (Hernandez-Castillo *et al.* 2003). This arrangement changed during the Late Permian (Changhsingian, 251 – 254 Ma) with the appearance of the Voltziaceae, when pollen cones became simple rather than compound and remained so to the present day. We know a great deal about the subsequent evolutionary changes in the seed cones as they diverged into different lineages. Some of these lineages gave rise to the great diversity seen in extant conifer families, whereas others became extinct. Derived from branching systems, the general trend can be described as a reduction and fusion of branches, but the compound structure (bracts and axillary seed scales borne on an axis) was retained. In several extant conifers, the

reduction proceeded to the possible limit of a single seed at the apex, the subtending bract and scale in the mature stage being eliminated or transformed. Detailed observations of ontogeny under Scanning Electron Microscopy (SEM) have revealed the basic structures and in some cases provide links with possible ancestral forms in the fossil record (Farjon & Ortiz-García, 2003). The fossil record also documents the demise of some conifer lineages at the great Permian–Triassic Extinction at about 250 Ma. The conifer family Voltziaceae appears to have survived the crisis and become diverse during the Triassic (200 – 251 Ma), only to disappear in the Early Jurassic. Its earliest representatives may have given rise to lineages leading to several modern families, as well as to families that went extinct later. By the Late Triassic, diversity of conifers was restored and thereafter exceeded that of the Palaeozoic. The Late Triassic (Norian, 203 – 216 Ma) Molteno sediment beds of the Karoo Basin in South Africa have yielded an extraordinary array of fossils, among which are many strange looking conifers (Anderson & Anderson 2003). Some can be assigned to extant families, such as the Podocarpaceae, whereas others appear to display or combine characters not found in living conifers. Among these species is a reconstructed small tree belonging to the Voltziaceae that grew on a river floodplain where it formed dense thickets. The extinct family Cheirolepidiaceae arose in the Late Triassic and later became one of the most diverse families, but disappeared by the end of the Lower Cretaceous. The Triassic Period produced taxa with apparent adaptations that no longer exist among conifers, such as tolerance to salinity (*Frenelopsis* (Schenk) emend. Watson and *Pseudofrenelopsis* Nathorst) and herbaceous ruderals, exemplified by *Aethophyllum stipulare* Brongniart from the Early Triassic Voltzia Sandstone of the Vosges Mountains in France (Rothwell *et al.* 2000). In the Jurassic (145 – 200 Ma) most of the extant conifer families appeared; the two that

arose earlier, in the Triassic, Araucariaceae and Podocarpaceae, had by then become diverse. As no recognisable angiosperms had yet arisen, conifers dominated the forests in the Jurassic, joined only by tree ferns, cycads and several species of *Ginkgo* L. This situation changed radically during the Cretaceous from the Barremian (125 – 130 Ma) onwards with the rise of the angiosperms, but conifer diversity remained high throughout the 80 million years of this Period. The fossil record usually remains uninformative about the environment in which shrubs and trees grew; almost all remains are found in sediments deposited in a wet environment a good distance from the location where the plants actually lived. But a general shift must have occurred, reminiscent of the present situation, in which the conifers often retreated to habitats marginal in terms of climate, availability of water and soil fertility. This marginalisation may have caused some species to become extinct, but serious reduction in species diversity only occurred much later. The fossil record shows that many conifers now confined to small populations, sometimes in just one or a few locations, were widespread during most of the Cenozoic until only a few million years ago. Examples are numerous, but most striking are the genera *Cathaya* Chun & Kuang, *Keteleeria* Carrière and *Pseudolarix* Gordon in Pinaceae and *Glyptostrobus* Endl., *Sequoia* Endl. and *Sequoiadendron* J. Buchholz in Cupressaceae — all once present across the temperate zone of the northern hemisphere, which during the Eocene reached into the High Arctic above 70°N. Conifers similar to *Sequoia* or *Sequoiadendron* were present during the Cretaceous and Cenozoic in the southern hemisphere as well. *Sciadopitys* Siebold & Zucc. (Sciadopityaceae), now confined to Japan, arose in the Jurassic in the supercontinent Laurasia and occurred in Europe until the Pliocene (2.6 – 5.3 Ma). We know all this from the fossil record (Beck 1988; Stewart & Rothwell 1993; Taylor *et al.* 2009).

Phylogeny

Phylogenetic studies of conifers began, as with all taxa, by analysing morphological characters, but by the late 1990s molecular (DNA) data had become the mainstream approach. Many papers retained a limited taxonomic scope, with Pinaceae and within it *Pinus* the most frequently studied. When a wider taxon sampling was applied, it was often in the context of a search for the phylogenetic position of a specific clade. An example of this approach is the search for the position of the subclass Gnetidae among the extant gymnosperms, often with conflicting results: (a) basal to all gymnosperms (Schmidt & Schneider-Poetsch 2002), (b) sister group to conifers (Bowe *et al.* 2000), (c) derived from conifers (Chaw *et al.* 2000),

and even (d) derived conifers and a sister group to Pinaceae (Hajibabaei *et al.* 2006). The second outcome represents the ‘gnetifer’ hypothesis; the latter two are variants of the ‘gnepine’ hypothesis, with paraphyly of conifers avoided in (c) and (d) by declaring Gnetidae to be conifers. Both (c) and (d) scenarios throw the baffling question of morphological and anatomical character evolution from conifers to gnetums up in the air, for others to solve (or not). None of these studies even suggest that the results could be artificial due to gaps in the taxon sampling (‘long branch attraction’ in cladistic terminology). More comprehensive analyses that sampled all conifer families started with Quinn *et al.* (2002), but not until Rai *et al.* (2008), and especially Leslie *et al.* (2012), were phylogenies of conifers based on large datasets in terms of both taxa and gene sequences. Morphology remained relevant to some workers, especially those who realised from their field of research, palaeobotany, that extant conifers treated at family or even genus rank are mere relicts of a much greater phylogenetic diversity that existed in the past. Morphology and cladistics obviously continued to be applied to extinct taxa only known from the fossil record, but Ohsawa (1997) argued that a similar approach is relevant in attempts to reconstruct phylogenies of extant conifer families. Gadek *et al.* (2000) combined morphological with molecular data to infer relationships within Cupressaceae (excluding fossils) but since then this approach has been discontinued. Given the essentially statistical nature of cladistic analysis, under a non-weighted treatment of characters, the molecular data are vastly more numerous and tend to overwhelm any signal that may come from morphology.

For phylogeny reconstruction, the fragmented nature of groups of extant conifers caused by extinction remains a persistent problem (aggravated by incompleteness of the fossil record if one wishes to include morphology), making classification more difficult (Christenhusz *et al.* 2011). At lower ranks, due to more comprehensive sampling of taxa (with vouchers more often correctly identified), more sequences from different genomes and genes, and greater computing power, resolution of clades has increased and become more stable. An example of this development are the species of *Araucaria* Juss., of which 14 (out of 20) are endemics of New Caledonia. The clade comprising the species of New Caledonia was in earlier analyses correctly related to *A. heterophylla* but it remained unresolved (e.g. Givnish & Renner 2004), whereas now we have a fully resolved tree for that clade and thus for the entire genus (Leslie *et al.* 2012). Basing a classification of conifers (or gymnosperms) on the results of phylogenetic analyses will remain a challenge for some time, but it is definitely an improvement on earlier, intuitive systems using only morphological characters.

Fig. 2. Phylogeny of extant conifer families. Podocarpaceae include Phyllocladaceae in this diagram.

Evolution

A commonly presented phylogeny of conifers (Pinophyta) is given in Fig. 2. The Pinaceae are basal in this phylogeny, but fossil evidence for this family appears much later in geological time than that of Podocarpaceae and Araucariaceae (Rothwell *et al.* 2012). Phyllocladaceae appear last and in most phylogenetic analyses are ‘nested’ within Podocarpaceae; the group could be derived from a podocarpaceous ancestor which lost its true leaves and developed an aril-like envelope around the seed, similar but not homologous with that of Taxaceae. No known conifer families appeared after the end of the Cretaceous (65.5 Ma) but none became extinct at the KT boundary either. From Table 1 it will be obvious that the extant families are only a fragmented sample of the total diversity of conifers that has arisen through time. Given the incomplete fossil record, with new discoveries continuously being made, we can expect this patchy representation to be even greater than it appears here.

The phylogeny presented in Fig. 2 therefore tells us rather little about conifer evolution and we will have to go back to the fossil record. Unfortunately, we have very few ‘whole-plant reconstructions’ from fossil remains (Bateman & Hilton 2009). However, ever since Florin (1951) we have progressively obtained an increasing understanding of the structure of the seed cones and their ovules/seeds, which may serve as crude proxies for whole plants. From

these remains we know that conifer evolution is marked by trends of sporadic organ reduction and/or suppression and fusion (Spencer *et al.* 2015). The recognition of homology in different characters remains challenging and requires identification of the genes influencing the characters and their ontogeny in comparable living organs (‘evo-devo’), as well as hypothetical transformation series as described by Florin and later researchers. Neither approach is without difficulties when it comes to distinguishing pattern from process (Spencer *et al.* 2015). At present, statements about character evolution remain speculative unless expressed in the most general terms, but we are gradually becoming more informed about the great diversity of adaptations and morphologies that existed throughout the 300 million years of conifer evolution. Some of these morphologies, such as wood anatomy and leaf arrangement and shape, could be remarkably conservative even over the entire length of time since conifers arose. Pollen cones, with some exceptions, also changed little over millions of years, as can perhaps be expected in wind-pollinated plants lacking opportunities to diversify by adapting to different pollinators. By contrast, seed dispersal mechanisms are even now highly variable in conifers, due to numerous adaptations connected with vectors of dispersal and hence resulting in different morphologies of seeds and cones. Reconstructing

Table 1. The 20 extinct and extant families of conifers, with their approximate first and last appearances in geological time. Families in **bold** are extant. Time scale after Ogg *et al.* (2008).

Family	First appearance	Ma	Last appearance	Ma
Thuydiaceae	Pennsylvanian (Gzhelian)	300	Lower Permian (Asselian)	297
Emporiaceae	Pennsylvanian (Gzhelian)	300	Lower Permian (Sakmarian)	290
Utrechtiaceae	Pennsylvanian (Gzhelian)	300	Lower Permian (Artinskian)	280
Ferrugliocladaeae	Lower Permian (Artinskian)	280	Lower Permian (Roadian)	270
Majoniaceae	Upper Permian (Roadian)	270	Upper Permian (Changhsingian)	252
Ullmanniaceae	Upper Permian (Capitanian)	263	Middle Triassic (Anisian)	240
Voltziaceae	Upper Permian (Changhsingian)	252	Lower Jurassic (Hettangian)	198
Podocarpaceae	Middle Triassic (Ladinian)	235	Present	
Cheirolepidiaceae	Late Triassic (Carnian)	225	Upper Cretaceous (Turonian)	91
Araucariaceae	Late Triassic (Norian)	210	Present	
Palyssiaceae	Late Triassic (Rhaetian)	202	Lower Jurassic (Sinemurian)	192
Pararaucariaceae	Middle Jurassic (Toarcian)	180	Middle Jurassic (Callovian)	163
Taxaceae	Middle Jurassic (Toarcian)	180	Present	
Cupressaceae	Middle Jurassic (Aalenian)	173	Present	
Sciadopityaceae	Middle Jurassic (Bajocian)	170	Present	
Cephalotaxaceae	Middle Jurassic (Bajocian)	170	Present	
Pinaceae	Upper Jurassic (Kimmeridgian)	155	Present	
Geinitziaceae	Upper Cretaceous (Turonian)	91	Miocene	20
Doliosdrobaceae	Upper Cretaceous (Maastrichtian)	68	Oligocene	30
Phyllocladaceae	Upper Cretaceous (Maastrichtian)	68	Present	

these morphologies from the fossil record could be a more rewarding approach to evolution than phylogeny reconstruction based on limited taxonomic data.

Taxonomy

Taxonomy involves the systematic evaluation of comparative data (Stuessy 2009). Its results are naming and classification of taxa; the basic unit is the species. According to Farjon (2010; 2nd edition 2017) there are 615 conifer species, but this number is more an estimate than a fact. It is highly dependent on the practice of species delimitation, or how one evaluates the comparative data. Two ‘competing’ recent compilations of conifers arrived at significantly different totals, Eckenwalder (2009) lower and Debreczy & Rácz (2011) higher than my number. For a very long time, taxonomists have elevated subspecies and varieties to species, or *vice versa*. New species have been described based on very limited material, later to be sunk by others into synonymy. One could perhaps argue that in due course these differences will even out as more data become available and methods to compare them improve, but I am not optimistic. As we have seen in the past, taxonomy is a very ‘democratic’ discipline with almost unlimited access to publication. We therefore have to contend with many species names of doubtful merit due to insufficient material and less than rigorous evaluation of comparative data. This ‘flux’ was in the past much more evident in the conifers of the temperate zone of the northern hemisphere than it is at present. The number of species in the largest genus, *Pinus*, seems now more or

less consolidated, albeit differing among the three workers mentioned above (Farjon: 113; Debreczy & Rácz: 127; Eckenwalder: 97). In contrast, the second-largest genus, *Podocarpus* L'Hér. ex Pers., with 97 species in Farjon and 82 species in Eckenwalder (Debreczy & Rácz exclude tropical conifers from their book), has been growing rapidly in number especially following the work of David de Laubenfels. Despite his not always meticulous species descriptions, de Laubenfels became the foremost expert on *Podocarpus* because few other taxonomists had a similar interest in the genus. If we could calculate the number of taxonomists per genus, those who have worked on *Pinus* would vastly outnumber all those who have researched any tropical conifer genus. With taxonomy in decline I do not see how this discrepancy can be overcome any time soon. The number of accepted genera in conifers has also increased substantially in recent decades and now stands at 70 according to Farjon (2010; 2nd edition 2017). This increase results mostly from a more detailed classification, elevating the rank for all conifers (a monophyletic group) from family in the early days of conifer classification to subclass in the latest scheme (Christenhusz *et al.* 2011). This now recognises three orders: Pinales, Araucariales and Cupressales according to the three clades evident in Fig. 2, with the families Pinaceae in the first, Araucariaceae and Podocarpaceae in the second, and Sciadopityaceae, Cupressaceae, Cephalotaxaceae and Taxaceae in the third. This classification is based almost entirely on phylogenetic studies evaluating molecular data and does not attempt to circumscribe the three orders in morphological terms (the families already had such descriptions). It may be difficult to provide simple

morphological circumscriptions given the widely disparate character states that characterise the families within two of the three orders. It also does not take into account the extinct families known from the fossil record. A first, but tentative, attempt to construct a scheme that includes both extinct and extant families was presented in Farjon (2008) but needs the input of a well-informed palaeobotanist such as Gar Rothwell to make it more robust. In such a classification the Pinaceae would no longer appear in the basal-most position or be ranked as a taxonomic order in the conifers. It is not common practice to include extinct taxa in a classification, but for conifers a classification of families of extant conifers is highly arbitrary without taking account of what is known from the fossil record.

Distribution

The distribution of the world's conifers has, until recently, been recorded very unevenly. Ecologists and foresters in North America and Europe have long been mapping the forest-forming species of the boreal and temperate climate zones in the northern hemisphere, using various data and methods. This work resulted in atlases such as those by Little (1971) for the United States and by Hegi (1981) for central Europe. The great atlas of Hultén & Fries (1986) covers only a few conifer species with far northern (Eurasian) distributions, but usefully incorporated data from numerous sources gathered over a long period. Few distribution maps at species rank were compiled for the southern conifers at this time. Distribution maps of families and genera world-wide were presented by Florin (1963), who compared these with the fossil record, and recently by Eckenwalder (2009); maps for species were given by Debreczy & Rácz (2011) but not world-wide. The first publication to present maps of all extant families, genera and species of conifers is Farjon & Filer (2013). There is another difference, too: all maps in the previous works cited are range maps. They depict the range of a taxon by shading the area where it occurs, or is inferred to occur, based on observations in the field or from the air. The atlas by Farjon & Filer is based on vouchered herbarium specimens with a stated collection locality; no shading is used to connect the resulting dots on the map. The completeness of the map is therefore dependent on the completeness in geographical terms of herbarium collections. For a reliable distribution pattern to emerge, not all localities of a species need to have been collected, but it is obvious that a reliable distribution pattern is not attainable for the boreal conifers, where collecting has been extremely patchy. The advantage of herbarium specimens is that they provide evidence of occurrence, albeit with a historical caveat: the species was present at the locality mapped

at the time of collection and this can have been more than a century ago.

Some distinct patterns of conifer distribution emerge from Map 1. In the northern hemisphere, the highest numbers of genera and species plus infraspecific taxa are found between latitudes 20° and 40° N, but in the southern hemisphere the latitudinal diversity is more variable. Here, conifer distribution is more fragmented, diversity being more localised and less influenced by latitude. South of the boreal forest zone (which would be filled with black dots if we had the specimens) conifers often follow the major mountain ranges. But they are also abundant in parts of Australia (outside the deserts), on the Malesian islands and well into the Pacific, in China and the eastern USA, where angiosperms dominate in the forests. Thinly spread in the UK, most of France and the low countries, they become more abundant in eastern Europe and on the Iberian Peninsula. Island archipelagos such as Japan and New Zealand have many conifers, whereas Madagascar has very few. Indeed, absence of conifers is perhaps more revealing, but sometimes also more puzzling, than presence. We note that deserts are devoid of conifers (but see the exception, *Cupressus dupreziana* A. Camus, in the centre of the Sahara). The steppe biome is also usually empty of conifers, but in Asia and North America some junipers can occur there. The Tibetan Plateau (the 'roof of the world') has no conifers and we can explain their absence as a result of uplift and concomitant climate change. But why should the Indian subcontinent have no conifers except a single species, *Nageia wallichiana* (Presl.) Kuntze, in the Western Ghats? For botanists who know Africa it will come as no surprise that conifers are uncommon there, too. But deserts aside, why are there no conifers in the Congo Basin? And across the Atlantic, they are absent in the Amazon Basin, too. The work on the *Atlas of the World's Conifers* discovered a wide gap in the Andes, across terrain entirely suitable for conifers that occur elsewhere in semi-arid regions, such as *Callitris* Vent. in Australia. But South America only has *Austrocedrus* Florin & Boutelje with adaptations to moderate drought and the climate in this section of the Andes is too harsh for it. In the Atlas (Farjon & Filer 2013) we discuss some probable explanations for these and other discontinuities in conifer distribution. India has a rich fossil record of Gondwanan conifers and other gymnosperms, but none are younger than the Late Cretaceous. Did they become extinct during the massive volcanism that laid down the Deccan Traps? Why did only one species (of Gondwanan origin and widespread in Southeast Asia) succeed in re-colonising the region during a period of 65 million years? All extant conifers in India are confined to the Himalayas and adjacent hills and came from the north; they are Laurasian conifers.

Map 1. Global distribution of all conifer species. The numbers of genera and taxa (species and infraspecific taxa) are calculated per 10 degree latitude band. The boreal conifer forests of Alaska, Canada, Scandinavia and Russia are shaded in this map to show their extent. Map EFR-2 in Farjon & Filer (2013).

Conifer diversity is unevenly spread (Map 2) and does not coincide with the overall distribution of conifer species shown in Map 1. Western North America, from SW British Columbia down to Honduras, is one region with many hotspots. Southern China and Japan are two other regions, and from there the hotspots are dispersed across Australasia (but avoiding Australia) all the way to New Zealand. Only two one-degree cells in eastern North America and two in Europe appear to harbour ≥ 10 taxa. Africa and South America have no one-degree cells with more than 7–8 species (in Africa these occur along the Mediterranean coast and in a phytogeographical sense are not really African). The causes of diversity in a one-degree square are

complex and the taxa can be relict species as well as the result of recent speciation. Extinction during the Pleistocene would explain the relative poverty in Europe, but not in eastern North America. The database used for the Atlas provides many data points for further analysis. Some of this is presented in the Atlas, but as computing and mapping (GIS) techniques improve, many other approaches await use by conifer researchers.

Ecology

The global distribution of conifers indicates that species occur in many different habitats. This is also

Map 2. The distribution of degree cells with ≥ 10 taxa. This map shows the areas and hotspots of conifer diversity at species and lower ranks. Map GTC-3 in Farjon & Filer (2013).

borne out by a great range in altitude, from sea level to 5,000 m in the Himalayas. Conifers form homogeneous forests or occur in forests with other trees, but also appear in scrubland, savannah and steppes and even in deserts. However, there is a general tendency for conifers to predominantly occur on soils or in climates that are suboptimal for plant growth. Many species that occupy these suboptimal sites in their natural habitat will do very well and often grow faster and taller when taken into cultivation on better sites. Conifers have adapted to survive under suboptimal conditions. One way they have done this is to establish a symbiotic relationship with fungi, forming ectomycorrhizal systems replacing the hair roots with fine hyphae and thereby extending the surface area for water and nutrient uptake up to 10,000 times. All conifers that have been investigated appear to have acquired elaborate mycorrhizal symbionts, often involving multiple species of basidiomycete fungi. As conifers have existed more than twice as long as angiosperms, it may be assumed that this symbiosis was well developed by the time of angiosperm arrival and subsequent dominance. Conifers have become evaders, avoiding competition from the ever more ubiquitous angiosperms by escaping into the short growing seasons of the northern latitudes or of high altitudes, or onto the nutrient-deficient sands and rocks, some such as ultramafic peridotite and serpentinite, toxic to most plants. In other situations, the mycorrhizal advantage can give conifers a head start in the pioneer phase of plant succession; once well-established they are able to compete with most angiosperm trees. More extreme examples of this strategy are found in some very long-living conifers, often becoming giant trees rising above the general canopy. Some individuals survive many cycles of disturbance and regrowth on site, thereby being first in spreading seeds on newly opened ground. They are pioneers and 'climax' trees at the same time and place. Renewal of these giant conifers occurs in episodes and is dependent on disturbance events that recur on a timescale of centuries (Enright & Hill 1995). In their natural habitat there are no angiosperms that can live as long or grow as tall. In several species, these events have over time led to the formation of metapopulations to which an extinction-recolonisation model might apply; examples are *Sequoiadendron giganteum* (Lindl.) J. Buchholz in California, *Fitzroya cupressoides* (Molina) I. M. Johnst. in Chile and Argentina, *Agathis australis* (D. Don) Lindl. in North Island, New Zealand and *Chamaecyparis formosensis* Matsum. in Taiwan. There seems to be ample scope for molecular approaches to explore the ecology of these conifers, from which we could perhaps learn how these remarkable adaptations have evolved.

Not all conifers are evaders; especially in tropical latitudes several species appear to occur as dispersed

individual trees in highly diverse angiosperm-dominated rainforests. Often, these species have morphological characters that are very similar to the other trees, such as broad, flat leaves, smooth or peeling bark needed to discard epiphytes, and perhaps most important of all, seed cones that seem to imitate fruits and thereby attract birds with their bright colours and succulent parts. They are capable of regenerating from seed under the canopy or in small gaps and seem to be at no disadvantage in relation to the angiosperms that surround them. Many species of *Podocarpus* belong in this category, as well as some other members of the Podocarpaceae. *Dacrycarpus imbricatus* (Blume) de Laub. and *Dacrydium xanthandrum* Pilg. are both tall canopy emergents in montane rainforest and have small leaves, those of the latter species even reduced to needles. Detailed studies of the ecology of these and other tropical conifers that seem to compete successfully with angiosperms are mostly lacking. The Podocarpaceae are apparently ancient (Table 1) and so it is possible that the notion that their seed cones imitate angiosperm fruits may be misplaced. Fossil evidence is unlikely to exist for these soft parts and so molecular ecology and phylogenetic studies are perhaps more informative approaches to address these questions.

The list in Table 2 is neither complete, nor is it certain for all species listed that they truly belong here. Ecology has not been studied in sufficient detail for many species and in several cases I have made inferences from habitat descriptions and/or field observations. In particular, some species may in fact be r -strategy trees instead of K -strategists. The distinction is further blurred by the fact that tree species can exhibit characteristics of both strategies, such as dispersal of many seeds (r -selection) combined with competitiveness and longevity (K -selection). The K -strategy trees do not invest in massive seedling establishment connected with large gap formation, most of which do not survive to maturity and of which only a few live to become large trees ready to renew the cycle. Instead they produce fewer offspring of which a larger proportion grows to maturity, competing for light and other resources with other trees, including angiosperms, that surround them.

Despite these caveats, it is obvious that the successful competitors of tall canopy angiosperms are predominantly found in the family Podocarpaceae. These conifers have succulent seed cones formed by an epimatium that envelops the single seed, or a receptacle that subtends it (Fig. 3). These structures are almost certainly adaptations to seed dispersal by birds and are similar to bird-eaten fruits in angiosperms. Only three conifers have dry, woody cones; these belong to other families. Most species also have more-or-less broad, flat leaves, but there are six species with

Table 2. Summary of conifers able to germinate and grow to >20 m canopy height under and among evergreen angiosperm trees, not requiring large gap formation for effective seed dispersal and establishment (i.e. *r*-strategy ecology) and not limited to nutrient-deficient soils.

Family	Species	Broad leaves	Scale/needle leaves	Succulent cones	Dry cones	Area
Cephalotaxaceae	<i>Cephalotaxus hainanensis</i> H. L. Li	Single veined		arillus		Hainan Island
Cephalotaxaceae	<i>Cephalotaxus mannii</i> Hook. f.	Single veined		arillus		Southeast Asia
Cupressaceae	<i>Callitris madagayana</i> (F. Muell.) F. Muell.		needles/scales		woody	NSW, Queensland
Pinaceae	<i>Keteleeria fortunei</i> (A. Murray bis) Carrière	Single veined			woody	Southern China
Pinaceae	<i>Pinus glabra</i> Walter		needles		woody	SE USA
Podocarpaceae	<i>Araucarioxylum dawsoni</i> (Stapf) C. N. Page	Single veined		epimatium		East Africa
Podocarpaceae	<i>Dacrydium imbricatum</i> (Blume) de Laub.		needles	receptacle		SE Asia, Malesia, SW Pacific
Podocarpaceae	<i>Dacrydium nauroriense</i> de Laub.		needles	epimatium		Fiji (Viti Levu)
Podocarpaceae	<i>Dacrydium nidulum</i> de Laub.		needles	epimatium		Malesia
Podocarpaceae	<i>Dacrydium xanthandrum</i> Pilg.		needles	epimatium		Malesia
Podocarpaceae	<i>Nageia nagi</i> (Thunb.) Kuntze	Multiple veined		epimatium		China, Japan
Podocarpaceae	<i>Nageia wallichiana</i> (C. Presl) Kuntze	Multiple veined		epimatium		Southeast Asia, Malesia
Podocarpaceae	<i>Podocarpus archboldii</i> N. E. Gray	Single veined		receptacle		New Guinea
Podocarpaceae	<i>Podocarpus bracteatus</i> Blume	Single veined		receptacle		Sunda Islands
Podocarpaceae	<i>Podocarpus crassigemma</i> de Laub.	Single veined		receptacle		New Guinea
Podocarpaceae	<i>Podocarpus elatus</i> R. Br. ex Endl.	Single veined		receptacle		Australia
Podocarpaceae	<i>Podocarpus guatemalensis</i> Standl.	Single veined		receptacle		Central/South America
Podocarpaceae	<i>Podocarpus matudae</i> Lundell	Single veined		receptacle		Mexico/Central America
Podocarpaceae	<i>Podocarpus milanjianus</i> Rendle	Single veined		receptacle		Tropical Africa
Podocarpaceae	<i>Podocarpus nerifolius</i> D. Don	Single veined		receptacle		SE Asia, Malesia, SW Pacific
Podocarpaceae	<i>Podocarpus oleifolius</i> D. Don	Single veined		receptacle		Central/South America
Podocarpaceae	<i>Podocarpus rubens</i> de Laub.	Single veined		receptacle		Malesia
Podocarpaceae	<i>Podocarpus rumphii</i> Blume	Single veined		receptacle		Malesia
Podocarpaceae	<i>Prumnopitys standleyi</i> (J. Buchholz and N. E. Gray) de Laub.	Single veined		epimatium		Costa Rica
Podocarpaceae	<i>Retrophyllyllum comptonii</i> (J. Buchholz) C. N. Page	Single veined		epimatium		New Caledonia
Podocarpaceae	<i>Retrophyllyllum vitiense</i> (Seem.) C. N. Page	Single veined		epimatium		Malesia, SW Pacific
Podocarpaceae	<i>Sundacarpus amarus</i> (Blume) C. N. Page	Single veined		epimatium		Malesia, Queensland
Taxaceae	<i>Torreya grandis</i> Fortune ex Lindl.	Single veined		arillus		China

Fig. 3. Conifer pseudo-fruits dispersed by birds. **A** *Cephalotaxus manii*; **B** *Nageia nagi*; **C** *Podocarpus elatus*; **D** *Podocarpus neriifolius*. PHOTOS: **A** L. AVERYANOV; **B, C** A. FARJON; **D** T. UTTERIDGE.

needles (all species are evergreen). The evolution of broad-leaved conifers in tropical and southern hemisphere forests may indeed have evolved in tandem with angiosperm ecological radiation (Biffin *et al.* 2012). Almost all species occur in tropical or subtropical forests in which angiosperms are usually diverse and dominant in terms of numbers of individual mature trees reaching the canopy. A common survival strategy among these podocarps is a delayed growth in height under canopy, followed by rapid growth when a large competing tree falls and creates a small gap admitting more light (Turner & Cernusak 2011).

Economic uses and importance

Conifers dominate industrial wood supply because of their technical and economic advantages for the wood-based industries, supplying well over 50% of the world's timber harvest (Cooper 2003). In plantation forestry, which provides a growing proportion of total industrial wood, conifers are preferred over angiosperms as they produce a much faster economic yield with more predictable shapes and sizes of timber. Nearly all conifer wood goes into pulpwood for the paper industry, although about two-thirds of conifers in the world's plantations are destined for timber. Some large-scale uses of the past, such as railway sleepers, mine props and fence posts, have been replaced by non-wood materials. Despite the encroachment of the digital age of electronic information, the demand for paper manufacturing is not diminishing, but recycling should also reduce the need for trees in paper making. On a global scale, the family Pinaceae far outweighs all other conifers in economic importance; among the genera in this family *Pinus* ranks first. Radiata pine (*Pinus radiata* D. Don) is a remarkable example: although very limited and threatened in its coastal Californian habitat, in plantations, particularly in New Zealand, it attains a conifer record growth in height of 2.5 m per year. Vast areas have been stripped of their native forest cover to be replaced by managed plantations of this pine in New Zealand, Chile, South Africa and elsewhere. There are also far more refined applications of pine wood especially that of valued species in subsection *Strobi* Loudon such as *P. lambertiana* Douglas and *P. monticola* Douglas ex D. Don that do not contain resin and are straight-grained.

The wood of Cupressaceae is very different in its properties from that of Pinaceae. The resistance to decay makes the wood of many species valuable for any outdoor application, from construction and carpentry to boat building. This is especially valued in Asian countries, with demand often exceeding (sustainable) supply, thus driving up prices. The fibrous long grain in the wood of several species allows big planks to be split without the use of saws,

causing large houses to be built by indigenous peoples ranging from the Alaskan coast to Vietnam. Temples in China, Korea and Japan traditionally make much use of cupressaceous wood. Most species do not naturally form vast forests and grow more slowly than many pines and spruces. An exception is *Cryptomeria japonica* (Thunb. ex L. f.) D. Don, which has become a major plantation tree in Japan, Taiwan and elsewhere in the Far East. Many other conifers produce valuable timber, such as kauri (Araucariaceae, *Agathis* Salisb.), but most constitute a limited natural resource and are not grown on a large scale in plantation forestry. Exploitation of these valuable conifer species is often to supply local or regional markets; international trade may be limited due to listings on the Appendices of CITES. Much more research is needed to investigate whether or not exploitation of this valuable conifer timber can be made sustainable (for relevant papers on Araucariaceae see Bieleski & Wilcox 2009).

The second-most economically important use of conifers is in horticulture. During the 19th century plant hunters employed by estate owners, or by associations working on their behalf, collected the seeds of many conifers in North America, China and other parts of the world to be planted in gardens and parks. The United Kingdom took a lead in this venture, but many other countries in Europe soon followed suit. Landowners took pride in their arboreta and vied with each other for the best collections, but also often exchanged plants. With its diverse topography and benign, cool climate, many species grow well in the UK; private ownership of much of the land and a national passion for growing exotic trees did the rest. The Victorian era was the heyday of this activity, but as fashions come and go, it did not last for very long. Going through a period of decline in the 20th century, it has seen a revival in recent decades, signalled by the growing membership in the International Dendrology Society (IDS) established in 1952. In economic terms this planting of conifers in parks has never been an important activity, but it probably stimulated an interest in conifers in the horticultural trade. Smaller conifers for smaller gardens, if they could be produced, meant more serious business. This led to the development of thousands of cultivars for gardens, grown in specialised nurseries and sold in garden centres. When 'dwarf conifers' did not remain as small as promised, demand passed through a deep trough, until more elaborate methods of selection and growing, making use of genetic bud mutations often found in witches' brooms, overcame this problem. Today, there is a thriving industry in many countries producing dwarf conifers suitable for small gardens and even high-rise balconies. Horticultural naming became more standardised under the rules of the International Code of Nomenclature for

Cultivated Plants (ICNCP) and the Royal Horticultural Society's International Conifer Register; the latter culminating in a massive, illustrated reference work (Auders & Spicer 2012). As the horticultural trade keeps renewing itself, cultivated conifers continue to be of economic importance.

Conservation

Under this heading fall several concerns about the natural world and its state of preservation, or decline. At the ecosystem level conifers can be keystone species, supporting many other species through the stages of their lives from seedling to old age and death. A decline of any kind can have detrimental effects on the functionality of that species in the ecosystem, leading to shifts in trophic cascades and ultimately to loss of biodiversity. This loss occurs where primary or 'old growth' forest is logged and replaced by more even-aged, younger stands of trees, even when the presence of the keystone species is maintained. Another concern is extinction of species. I shall concentrate on that aspect in this review. For 20 years, from 1995 to 2015, I chaired the Conifer Specialist Group of IUCN-SSC and we assessed the conservation status, or threats of extinction, of all conifer species twice during that period. The interval between assessments was roughly 15 years, the results of the first assessment being published in 1999 (Farjon & Page 1999). At that time, c. 25% of all taxa at species and infraspecific ranks were considered to be threatened with extinction (categories CR, EN and VU). The second assessment used refined criteria (version 3.1 of 2001) and was conducted over the period 2011 – 2014. Again, all taxa were evaluated and a larger proportion of taxa was found to be threatened; calculated at species rank, 34% came under the threatened categories (search 'conifers' in *The IUCN Red List of Threatened Species*TM 2016-3) (Table 3).

The steep rise in the proportion of threatened species (taxa) over this short period can be attributed to several causes. In a Red List Index assessment, conducted in early 2016, we attempted to separate changes in conservation status between the two assessments due to artificial causes (more information, changes in criteria) from genuine changes. The vast majority of changes in the status of conifer taxa can be attributed to more detailed information being available for the second assessment, combined with more sophisticated methods of estimating risks; for example

by using calculations of extent of occurrence (EOO) and area of occupancy (AOO) based on the mapping of species conducted for the *Atlas of the World's Conifers* (Farjon & Filer 2013). These changes do not represent genuine changes in the level of threat to a species. Only 33 species with a changed conservation status were found to have changed due to modifications of their natural environment. For all but one species, there has been a downward trend; species have moved up at least one category of threat in the 15 years since the first assessment. Deforestation, logging and general habitat deterioration were found to be the major causes, but in California increased incidence and severity of wildfires was the most significant factor.

The distribution of threatened conifer taxa shown in Map 3 is mostly consistent with the distribution of diversity hotspots shown in Map 2. However, as can be expected, threatened conifers are not limited to these areas of high diversity. South America, and also SE USA and the West Indies, while not attaining a diversity of 10 taxa in any one-degree cell, score high for threatened taxa. Africa, Madagascar, Europe and Australia also have a disproportionate level of threatened conifers. The one-degree cell that scores highest contains 37 species, of which three are classified as Critically Endangered (CR), 11 as Endangered (EN) and six as Vulnerable (VU). This cell is located in the Montagne des Sources/Rivière Bleue area of SE New Caledonia. Such data analysis can be used in the planning of protected areas (Farjon & Filer 2013).

Future research

Research in almost all disciplines with conifers as the subject will continue into the future. My aim here is to indicate where the knowledge we have obtained so far is still falling short of what is needed for a more complete understanding of conifer biogeography and systematics, and related subjects such as ecology and conservation. An analysis of the collection dates for specimens of Podocarpaceae presented in Farjon & Filer (2013: 474 – 475) shows a peak for the decade 1961 – 1970 and a sharp decline thereafter. The decline is not evenly distributed, but appears to be most prevalent in Africa and South-East Asia and less obvious in Central and South America. The historical nature of herbarium collections can make inferences from them about current distribution of a species problematic, as was demonstrated in a case study of the island of Sumatera by MSc students presented in

Table 3. Numbers of species in the different IUCN Red List Categories as per the second assessment.

CR	EN	VU	NT	LC	DD	NE	Total
28	103	80	93	296	7	8	615

Map 3. The distribution of threatened (pink and red) and non-threatened (white) conifer taxa according to their categories of threat on the IUCN Red List in one-degree cells. Red List significance in the threatened categories (VU, EN, CR) is indicated in two classes, red being the highest. Map EFR-4 in Farjon & Filer (2013).

the Atlas (Farjon & Filer 2013: 480 – 482). Large areas of Malesia remain virtually unknown territory for conifer occurrence, including much of western New Guinea (excluding the Kepala Burung/Bird's Head Peninsula and two areas in the central mountain range Pegunungan Maoke), the Moluccas, Borneo (except Sabah), Sumatra (lacking recent collections) and Timor. As Indonesian efforts are insufficient for the task, institutions from collaborating countries should become involved. Another region still inadequately known for conifers is the tepuis region of the Guiana Highlands in Venezuela, Guiana and Brazil. More endemic species are to be expected there, most likely in the genus *Podocarpus*. Species distribution models (SDMs) based on existing occurrences from georeferenced herbarium collections and (a)biotic predictors may help to narrow down areas to be surveyed for conifer species. This could lead to discovery of new taxa based on new finds in the field. Taxonomic revisions seem to have gone out of fashion, but the fact that such revisions have been unevenly applied to conifer families, with Podocarpaceae as the Cinderella among them, means that detailed knowledge of this family is lacking. A thorough taxonomic revision is the basis for all other research dealing with genera and species; without it other studies become unreliable. A complex family like this one, with many species just known from 1 – 5 collections in remote tropical forests, requires dedicated team effort if it is to deliver a monograph within reasonable time. Phylogenies based on comprehensive sampling of taxa and genes are now becoming available (e.g., Leslie *et al.* 2012) but can be improved, especially when a revision of Podocarpaceae becomes available. As with taxono-

my, here, too there is a bias towards families and genera represented in the northern hemisphere. A revision and new phylogeny of Podocarpaceae should go hand-in-hand, with mutual enhancement of the results. This family should then also become a focus for ecological research — for example into the question of adaptation and competition strategies of species listed in Table 2, which seem to have overcome the necessity of angiosperm evasion by becoming *K*-selected trees.

Molecular studies, including but not limited to phylogenetic relationships, could provide answers to questions regarding how these adaptations evolved. Understanding the ecology of conifers is key to the development of sustainable management and use of forests in which conifers occur. Such understanding may lead to the realisation that some coniferous forests should be left to develop without interference from people, whereas in others limited selective logging, taking into account all that is known of forest dynamics and the niche requirements of animals, fungi and plants that are known to be dependent on the ecosystem, can safely be allowed. Given the depletion of forest ecosystems in many parts of the world, and the threats with extinction posed to many conifer species, the discipline of restoration ecology is becoming more important than ever before, and here, too I believe there is a need for increased research efforts.

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