

Original Article

In search of lost time: tracing the fossil diversity of Podocarpaceae through the ages

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ABSTRACT

The Podocarpaceae are a morphologically diverse conifer family that have a cryptic fossil record reported since the Permian. We reviewed the fossil record of Podocarpaceae, tested the affinities of its oldest records using phylogenetic analyses, compiled macrofossil occurrence records, and investigated the diversity, distribution, and morphology of Podocarpaceae through time. We found that Permian, Triassic, and some Jurassic fossils referred to Podocarpaceae should not be placed in the family. Our total-evidence phylogenetic analyses, which sampled all major conifer lineages, recovered the Triassic *Rissikia* and the Jurassic *Nothodacrium* as stem-group conifers and the Jurassic *Mataia* as part of the Araucariales stem group. We further discuss the phylogenetic position of the Mesozoic enigmatic conifers *Pararaucaria* (Cheirolepidiaceae) and *Telemachus* (Voltziales), which were recovered most frequently in the conifer stem group. We conclude that the earliest reliable Podocarpaceae occurrences are from the Jurassic of both hemispheres and have scale-like leaves. Most extant genera appear in the fossil record between the Late Cretaceous and the Early Cenozoic. Many extant leaf morphologies appear in the Early Cretaceous, coeval with angiosperm diversification, consistent with the hypothesis that expanded leaves in Podocarpaceae are adaptive responses for light harvesting in angiosperm-dominated environments today.

INTRODUCTION

The conifers are the largest group of living gymnosperms, with a long and complex evolutionary history and a rich fossil record that extends into the Carboniferous and encompasses broad morphological and ecological diversity. Among the six living conifer families, the Podocarpaceae stand out for their unusual and highly diverse morphology and enigmatic evolutionary history (de Laubenfels 1953, 1969a, b, 1972, Brodribb 2011, Biffin *et al.* 2012, Knopf *et al.* 2012, Farjon 2017). The Podocarpaceae are the second most speciose conifer family, comprising *c.* 200 species in 17–19 genera (Knopf *et al.* 2012, Farjon 2017, Page 2019) that inhabit some of the most diverse and endangered environments on Earth (Farjon 2017), including tropical montane regions of the Southern Hemisphere. Today, the family exhibits a mainly Gondwanan distribution (Florin 1963, Knopf *et al.* 2012, Farjon 2017), but the geologic record reveals Mesozoic and Cenozoic occurrences from both hemispheres (Supporting Information, Tables S1–S3 in Appendix S1).

The Mesozoic fossil record of Podocarpaceae has proven difficult to interpret and reconcile with living lineages, owing in part to the morphological diversity of photosynthetic and ovulate organs in extant genera (de Laubenfels 1969a, b, 1972, Brodribb 2011, Farjon 2017), the derived nature of this morphology within conifers, and the distribution of these traits in the fossil record and among extant species. Notably, many Podocarpaceae are characterized by specialized vegetative organs and highly reduced ovulate cones, components of which are modified into fleshy structures that attract seed dispersers (de Laubenfels 1969a, b, 1972, Farjon 2017). These traits appear in the fossil record of the family during the Cretaceous and Cenozoic (Supporting Information, Tables S2, S3 in Appendix S1). The ancestral morphology of the family is uncertain, with many older occurrences remaining equivocal. As a result, there are substantial gaps in our understanding of the evolution and fossil record of Podocarpaceae.

Salient questions pertain to the appearance of the family in the fossil record, the ancestral morphology of Podocarpaceae,

and the morphological changes involved in the evolution of the crown group. Most attempts to address such questions have focused exclusively on living members (e.g. Biffin *et al.* 2011, Klaus and Matzke 2019), with fossils usually incorporated as node calibrations in divergence-time analyses (e.g. Biffin *et al.* 2012, Leslie *et al.* 2012, 2018, Quiroga *et al.* 2015), although some recent studies have used Cenozoic fossils as terminals in phylogenetic reconstructions (Greenwood *et al.* 2013, Andruchow-Colombo *et al.* 2019a, b). Important steps in resolving the puzzling origins of Podocarpaceae include critical re-evaluation of the fossil record and phylogenetic analyses that reveal stem-group members of the family, as well as of the order Araucariales (Podocarpaceae + Araucariaceae).

Extensive reviews of the fossil record have been published for other conifer families (Stockey 1982, 1994, Panti *et al.* 2012, Araucariaceae; Stockey *et al.* 2005, Cupressaceae; Taylor *et al.* 2009, Pinaceae; Alvin 1982, Watson 1982, 1988, Cheirolepidiaceae), but no exhaustive reviews have been published for Podocarpaceae as a whole (for regional or genus-specific treatments, see: Hill 1989, Hill and Brodrigg 1999, Andruchow-Colombo *et al.* 2019b). In this context, reviewing the fossil record of Podocarpaceae constitutes a necessary step for understanding deep-time evolutionary patterns and the origin of the unique morphologies of extant representatives. Moreover, a comprehensive review is necessary to provide reliable fossil calibrations for divergence-time analyses.

Here we review the macrofossil record referred to Podocarpaceae (excluding wood) from the earliest reports in the Permian to the Pleistocene. We discuss whether the earliest records are compatible with the family and test their affinities using total-evidence phylogenetic analyses encompassing all major extant and extinct conifer lineages. We also discuss the age of appearance of the different reproductive and vegetative morphologies, as well as biogeographic patterns observed in the fossil record and interpret them in the light of major ecological and biotic events. Additionally, we provide stratigraphic ranges for extant and extinct genera and a diversity analysis of Podocarpaceae through time.

MATERIALS AND METHODS

Phylogenetic analysis

Total evidence matrix

The total evidence matrix analysed here is based on that of Matsunaga *et al.* (2021) extensively modified here by addition, elimination, and modification of characters and states (as detailed in Supporting Information, Appendix S2B). We added six extant species of six genera of Podocarpaceae (*Saxegothea conspicua*, *Microcachrys tetragona*, *Pherosphaera hookeriana*, *Retrophyllum rospigliosii*, *Lepidothamnus laxifolius*, *Lagarostrobos franklinii*), and three fossil taxa referred to Podocarpaceae and considered here to have uncertain affinities with it: the Late Triassic *Rissikia media*, and the Jurassic *Nothodacrium warrenii* and *Mataia podocarpoides* (Townrow 1967a, b).

The complete taxon sampling comprises 49 species, including *Ginkgo biloba* to root the tree, 11 extant Pinaceae, three Araucariaceae, 11 Podocarpaceae, seven Cupressaceae, and one of each of Taxaceae and Sciadopityaceae; as well as

14 extinct conifer species (Supporting Information, Appendix S2A). The fossil taxa included in this analysis are *Hanskerpia hamiltonensis* (Pennsylvanian, Voltziales; Rothwell *et al.* 2005), *Cordaixylon dumusum* (Pennsylvanian, Cordaitales; Rothwell 1993), *Emporia lockardii* (Pennsylvanian, Voltziales; Mapes and Rothwell 1984, 2003, Rothwell *et al.* 2005), *Voltzia hexagona* (Permian, Voltziales; Schweitzer 1966), *Telemachus aequatus* (Middle Triassic, Voltziales; Yao *et al.* 1997, Bomfleur *et al.* 2013), *Rissikia media* (Late Triassic, ?Podocarpaceae; Townrow 1967a), *Nothodacrium warrenii* (Early–Middle Jurassic, ?Podocarpaceae; Townrow 1967b), *Pararaucaria patagonica* (Middle Jurassic, Cheirolepidiaceae; Escapa *et al.* 2012), *Schizolepidopsis daohugouensis* (Middle–Late Jurassic, Pinaceae; Zhang *et al.* 2011), *Mataia podocarpoides* (Late Jurassic, ?Podocarpaceae; Townrow 1967a), *Eathiestrobos mackenziei* (Late Jurassic, Pinaceae; Rothwell *et al.* 2012), *Schizolepidopsis ediae* (Early Cretaceous, Pinaceae; Matsunaga *et al.* 2021), *Schizolepidopsis canicularis* (Early Cretaceous, Pinaceae; Leslie *et al.* 2013), and in some analyses also *Schizolepidopsis longipetiolus* (Early Cretaceous, Pinaceae; Xu *et al.* 2013).

The morphological block of the matrix includes 70 characters from seed cone morphology (Supporting Information, Appendix S2B), as this organ is considered to be the best proxy for whole-plant concepts in conifers (Spencer *et al.* 2015). The matrix was uploaded to Morphobank (P4361; <http://morphobank.org/permalink/?P4361>) and is also provided in Supporting Information, Appendix S3. There are 13.7% missing entries (460 cells) and 27.7% missing (inapplicable) data (931 cells) in the morphological block of the matrix.

Three alternative morphological characters were created to capture the variation in the number of ovuliferous complexes per cone. Character 66, *Number of ovuliferous complexes in the seed cone*, is a discrete character with five states that tend to show differential distribution among families (see Supporting Information, Appendix S2A). The other two alternative characters are meristic (character 0) and continuous (character 1), corresponding to the number of ovuliferous complexes per cone (character 0) and its logarithm with base 10 (character 1) (see Supporting Information, Appendix S2D). These two alternative characters make different assumptions about character evolution. Character 0 ranges from 1 to 250 ovuliferous complexes per cone (see Supporting Information, Appendix S2D) and assumes that transitions between any two consecutive states (e.g. 1 and 2, or 233 and 234) are equally important (i.e. equally costly) and thus equally informative. Its logarithmic transformation (character 1) was performed to create a continuous character for which changes occurring in the lower end of the range are more costly than those on its higher end (see Supporting Information, Appendix S2B, D). Character 1 is potentially a more realistic assumption because genera with fewer ovuliferous complex show less intrageneric variation in this trait than genera with high numbers of ovuliferous complexes (e.g. *Retrophyllum* 1, *Pherosphaera* 3–8, *Sciadopitys* 15–40, *Cryptomeria* 20–30, *Wollemia* 100–150). Therefore, changes in ovuliferous complex number are generally less phylogenetically informative at the high end of the range than at the low end. Characters 0, 1, and 66 were never active at the same time in a single analysis since they reflect the same seed cone trait. Instead, they were alternatively activated in different analyses to test how the treatment of this character influenced the placement of the fossils (see following subsection).

The molecular blocks of the matrix include 7253 characters (1479 informative for parsimony, 20.4%) from the nuclear regions 18S (1824 characters, 160 informative for parsimony, 8.8%) and *PHYP* (2402 characters, 681 informative for parsimony, 28.4%); and the plastid regions *matK* (1599 characters, 838 informative for parsimony, 52.4%) and *rbcL* (1428 characters, 70 informative for parsimony, 4.9%). The analysed DNA regions were downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>; for accession numbers see [Supporting Information, Appendix S2C](#)) and were aligned and formatted with GB-to-TNT ([Goloboff and Catalano 2012](#)), using MAFFT v.7.487 ([Katoh et al. 2002](#), [Katoh and Standley 2013](#)) as the alignment software under default parameters. Accessions were based on those used by [Matsunaga et al. \(2021\)](#). The resulting combined matrix has 49 taxa and 7323 characters of DNA and seed cone morphology ([Supporting Information, Appendix S3](#); sequence alignments provided in [Appendix S4](#)).

Maximum parsimony analyses

The matrix used for the parsimony analyses excluded the fossil species *S. longipetiolus* because it behaved as a rogue taxon and complicated the interpretations of other relationships.

Maximum parsimony searches were conducted under a wide variety of conditions as a sensitivity analysis testing the robustness of phylogenetic topologies pertaining to key taxa to different analytical assumptions. The parsimony analyses were performed in TNT 1.5 ([Goloboff et al. 2003, 2008](#), [Goloboff and Catalano 2016](#)) with a range of conditions including equal weights and extended implied weights ([Goloboff 1993, 1997, 2013](#)) with four alternative concavity constant values ($k = 3, 6, 12, 15$). Implied weights penalize homoplastic characters by lowering their weight ([Goloboff 1993, 1997, 2013](#)). Weighting strength depends on the values assigned to the concavity constant (k), low k -values result in stronger penalizations on homoplastic characters, whereas higher k -values result in analyses closer to an equal weights approach ([Goloboff 1993, 1997, 2013](#)). All discrete characters were treated as unordered, except for two that were treated as additive: *Degree of fusion of scale elements* (character 63) and, in some analyses, *Number of ovuliferous complexes in the seed cone* (character 66), as they are discretized continuous and meristic characters respectively with an arguably intrinsic order. For each analysis, only one of the characters reflecting the ovuliferous complex number per cone (0, 1, or 66) was active. The discrete character (66) was alternatively treated as ordered or unordered, whereas the meristic (0) and continuous characters (1) were standardized ([Thiele 1993](#), [Goloboff et al. 2006](#)) with two alternative maximum single transformation scores: 1 and 5. Standardization to 1 is typical in phylogenetic studies including continuous characters ([Escapa and Catalano 2013](#)), whereas the standardization to 5 follows the number of states in the discretized version of the character (character 66). Each analysis was performed alternatively with and without a monophyly constraint of the two main clades within Pinaceae (Abietoideae and Pinoideae-Piceoideae-Laricoideae), always allowing for floating fossil taxa (i.e. fossil taxa are not restricted in or out of these clades). The constraint was implemented because otherwise *Cedrus* was placed as sister to the rest of Pinaceae, rather than in the abietoid clade as in other studies and Bayesian

analysis of the same data. All other extant relationships were consistent with previous studies. The combination of parameters outlined above resulted in a total of 60 analyses: five weighting schemes, with three different characters alternatively activated (0, 1, 66), each with two alternative ordering/standardization conditions, with and without the constraint on the main clades of Pinaceae ([Supporting Information, Appendix S4](#)).

Searches were conducted by an initial round of random addition sequences, followed by tree-bisection-reconnection (TBR) rearrangements and a combination of sectorial searches and tree fusing (as set by default under the command *xmult*), setting the stop after reaching the minimum length 50 times. An additional round of TBR rearrangements was performed from the trees obtained in the first round of the analysis. The strict consensus of all the most parsimonious trees was calculated.

To aid in visualizing the different relationships recovered for fossil taxa across all analytical conditions, a phylogenetic consensus network was constructed with all most parsimonious trees of the 30 analyses that had a monophyly constraint for the Pinaceae main clades (66 trees) using SplitsTree 4.18.3 ([Holland and Moulton 2003](#), [Huson and Bryant 2006](#)), with a threshold of 0.1, meaning that the relationships shown in the resulting network are those that appear in at least a 10% of the most parsimonious trees of the 30 analyses. To facilitate the view of all connections, the consensus network was not weighted, therefore there is no differentiation between commonly and rarely recovered relationships. Most common connections will be represented in a tree diagram ([Fig. 1](#)).

The tree diagram presented, here referred as a ‘meta-consensus’, shows the relationships recovered in a total of 161 trees obtained from the 60 analyses performed. Relationships among extant Pinaceae are represented as in the constraint analyses, but all other relationships are based both on constraint and unconstraint trees. In this meta-consensus, we show the alternative placings of rogue fossil taxa with a full line for the most common position and a broken line for the less common positions. Next to each placing of the rogue taxa there is a bar indicating the percentage of analytic conditions that resulted exclusively in that position (i.e. single most parsimonious position), followed by the percentage of analyses in which that position was recovered in at least some of the optimal trees. A summary of the conditions for each recovered position is provided in the tree diagram, and further detailed in the [Supporting Information, Appendix S4](#).

Bayesian analysis

The Bayesian analysis of the total evidence matrix was performed with *MrBayes* ([Huelsenbeck and Ronquist 2001](#), [Ronquist et al. 2012](#)) in the CIPRES Science Gateway ([Miller et al. 2010](#)). Tree searches were performed using two parallel runs of Metropolis-coupled Markov chain Monte Carlo consisting of three hot and one cold chain, with chain length set to 20 million generations per run. Runs were sampled every 2000 generations, for a total of 10 000 sampled trees for each parallel run. The morphological partition was analysed using the Mk model of morphological evolution, corrected for ascertainment bias, with gamma-distributed between-character rate variation ([Lewis 2001](#)), whereas the four molecular partitions, corresponding to each molecular marker,

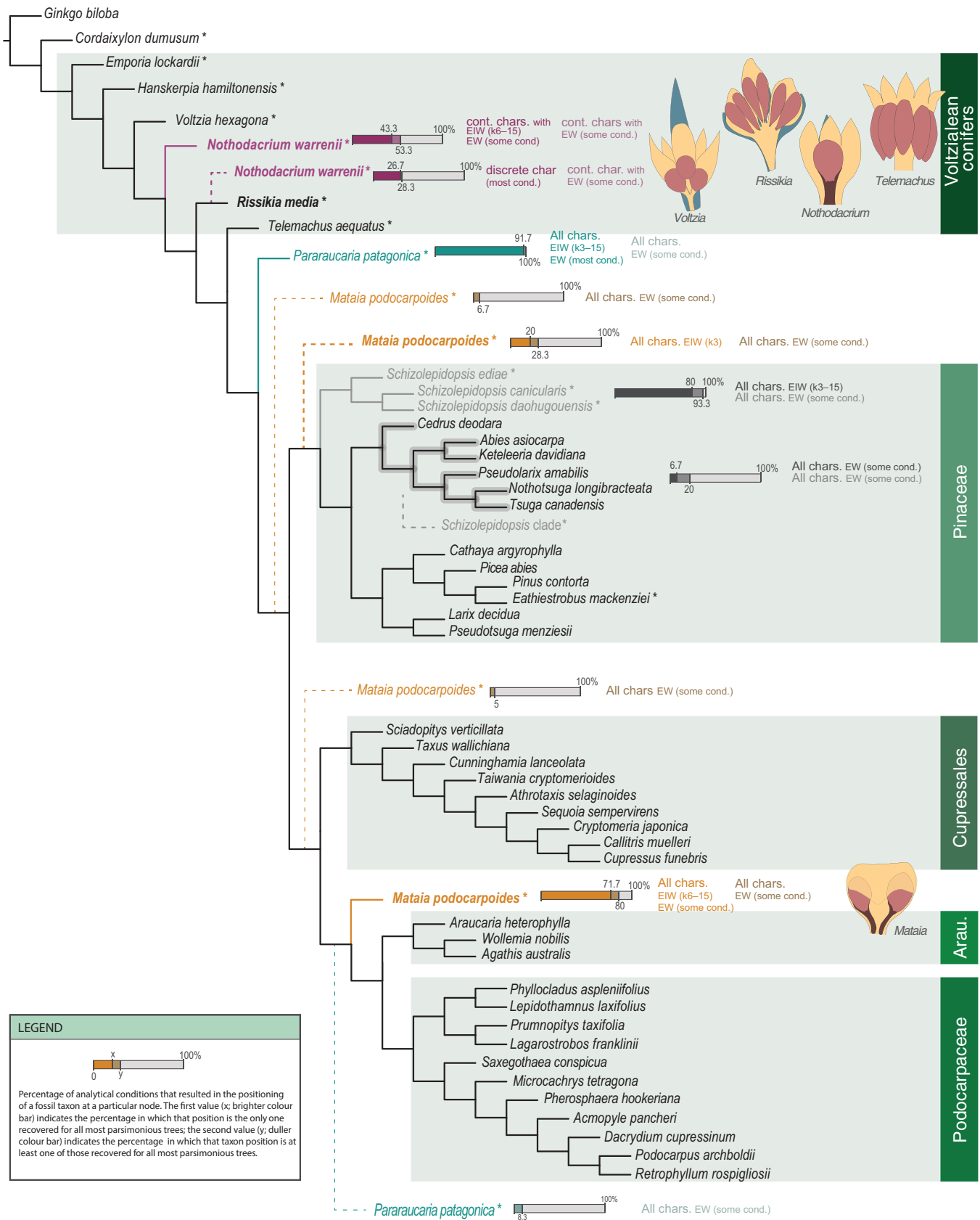


Figure 1. Meta-consensus tree of 161 trees obtained in 60 parsimony total evidence analyses. Relationships among extant Pinaceae are represented as in the analyses with a constraint of the two main clades within Pinaceae (Abietoideae and Pinoideae-Piceoideae-Laricoideae) showing the alternative positions of unstable taxa among analyses. All fossil taxa are indicated with an asterisk. In every case, solid lines indicate the placements most commonly recovered for each of the unstable taxa (taxa in colour), whereas dashed lines indicate less common

were analysed using a GTR+ Γ model (Supporting Information, Appendix S4). Each run was assessed visually in Tracer v.1.7.2 (Rambaut *et al.* 2018) to ensure convergence and adequate effective sample sizes of all parameters. The first 25% of trees were discarded as burn-in and the resulting sampled trees were summarized using an all-compatible majority-rule consensus (a 50% majority rule consensus with all compatible groups added to the tree, Huelsenbeck *et al.* 2015).

Per limitations of the software, the following character treatments were implemented: polymorphic scorings were treated as missing entries; only the discrete version of the number of ovuliferous complexes was used (i.e. character 66); all characters were treated as unordered.

A consensus network was constructed with the trees sampled of the Bayesian analysis (15 000 trees) using the software SplitsTree 4.18.3 (Holland and Moulton 2003, Huson and Bryant 2006), with a threshold of 0.2 (relationships shown in the network appear in at least 20% of the trees).

Diversity curves

To visualize fossil diversity through time, we generated diversity curves at both genus and occurrence level. The diversity curves were based on 207 taxa (Supporting Information, Appendix S5), which are a subset of those in the Supporting Information (Tables S1–S3 in Appendix S1). For building the curves, we excluded older taxa with uncertain affinities (Jordan Permian taxon, *Rissikia*, *Rissikianthus*, *Rissikistrobus*, *Mataia*, *Nothodacrium*; Tables S1, S2 in Appendix S1; see Discussion) and records uncertain due to incomplete preservation (?Podocarpaceae megastrobilus, Mildenhall 1976; Table S2 in Appendix S1). Records referred to the form genera *Podostrobus* and *Elatocladus*, to morphotypes without formal names, or associated with more than one genus (*Dacrydium* vel *Halocarpus*, Fontes and Dutra 2010; Table S3 in Appendix S1) were included in occurrence calculations but excluded from genera calculations. *Protophyllocladus* was excluded from the diversity calculations owing to its dubious affinity with the family, as discussed by many authors (Seward 1904, Florin 1940a, Tanai 1979, Andruchow-Colombo *et al.* 2019b, Dörken *et al.* 2021; but see Nosova and Golovneva 2014).

An ‘occurrence’ is considered as the report of a particular species (formally named or not) in a particular locality. For each occurrence, the midpoint of its age range was registered following the most recent age constraints for the locality of origin and other relevant considerations in the literature (Supporting Information, Appendix S6). The age point was then assigned to the corresponding geologic stage/age following the 2021/07

Chronostratigraphic chart (Cohen *et al.* 2013 updated), and it was registered in a table under the midpoint age of its stage/age (Supporting Information, Appendix S5). Therefore, the maximum resolution considered here is that of stage/age.

For estimating the number of extant genera through time, the earliest certain occurrence was considered as the biochron starting point and extended to the present; for fossil genera, the first and last occurrences were used to define the biochron. For observed occurrences, only the stages/ages in which a taxon was recorded are considered. Calculations were made in Microsoft Excel.

Terminology

The extinct order Voltziales is most likely non-monophyletic, with many species possibly belonging to the conifer stem group (this work; Matsunaga *et al.* 2021). We do not address the taxonomic status of Voltziales or its members. Despite this, it remains necessary to have a term to encompass this morphologically distinctive group (Florin 1954), and so herein we informally refer to relevant taxa as ‘voltziales’.

When a genus was split into two or more genera but there is no literature addressing the treatment for fossil species previously described within the original genus, we clarify to which genus we consider the fossil species to belong by adding the new generic name in square brackets between the original generic assignment and the epithet. For example, *Podocarpus* [*Dacrycarpus*] *dubius* was originally described as *Podocarpus*. *Podocarpus* was later split in several genera, including *Dacrycarpus*, which we argue is the correct generic name for the fossil currently.

RESULTS

Phylogenetic analysis

Parsimony analyses

The maximum parsimony analyses of the combined matrix resulted in 1–15 most parsimonious trees depending on the search conditions (Summary Table in Supporting Information, Appendix S4). Most analyses resulted in one or a few optimal trees, and therefore in a single configuration of the fossil taxa. A meta-consensus showing most common positions of unstable fossil taxa across different analyses is shown in Figure 1.

Mataia podocarpoides was recovered in most analyses as sister to the crown group Araucariales (Fig. 1 orange full line). The analyses that resulted in that position were performed under extended implied weights with moderate to low weighting force ($k = 6–15$) and some analyses under equal weights (Summary Table, Supporting Information, Appendix S4). Most equal

positions; bars next to the unstable taxa indicate the percentage of analyses that recover that position in all most parsimonious trees (brighter colour, value above the bar, x in the legend) and in at least some of the most parsimonious trees (duller colour, value below the bar, y in the legend). For example, for *Mataia podocarpoides* bars contain orange and light brown: orange represents the percentage of analyses recovering that position in all most parsimonious trees (i.e. analyses for which there was a single most parsimonious position); brown represents the percentage of analyses in which a given position of *Mataia* was recovered in at least a subset of the most parsimonious trees. In the instances where only brown bars are shown, that position was only recovered as one of the most parsimonious alternatives, but never as the solely option in an analysis. Note that the *Schizolepidopsis* clade has several alternative positions within the abietoid clade of Pinaceae (see Fig. 2B), indicated with a thicker grey line. The voltziales conifers show several different arrangements in the most parsimonious trees, the most common are depicted here, the remaining alternatives can be seen in Figure 2A.

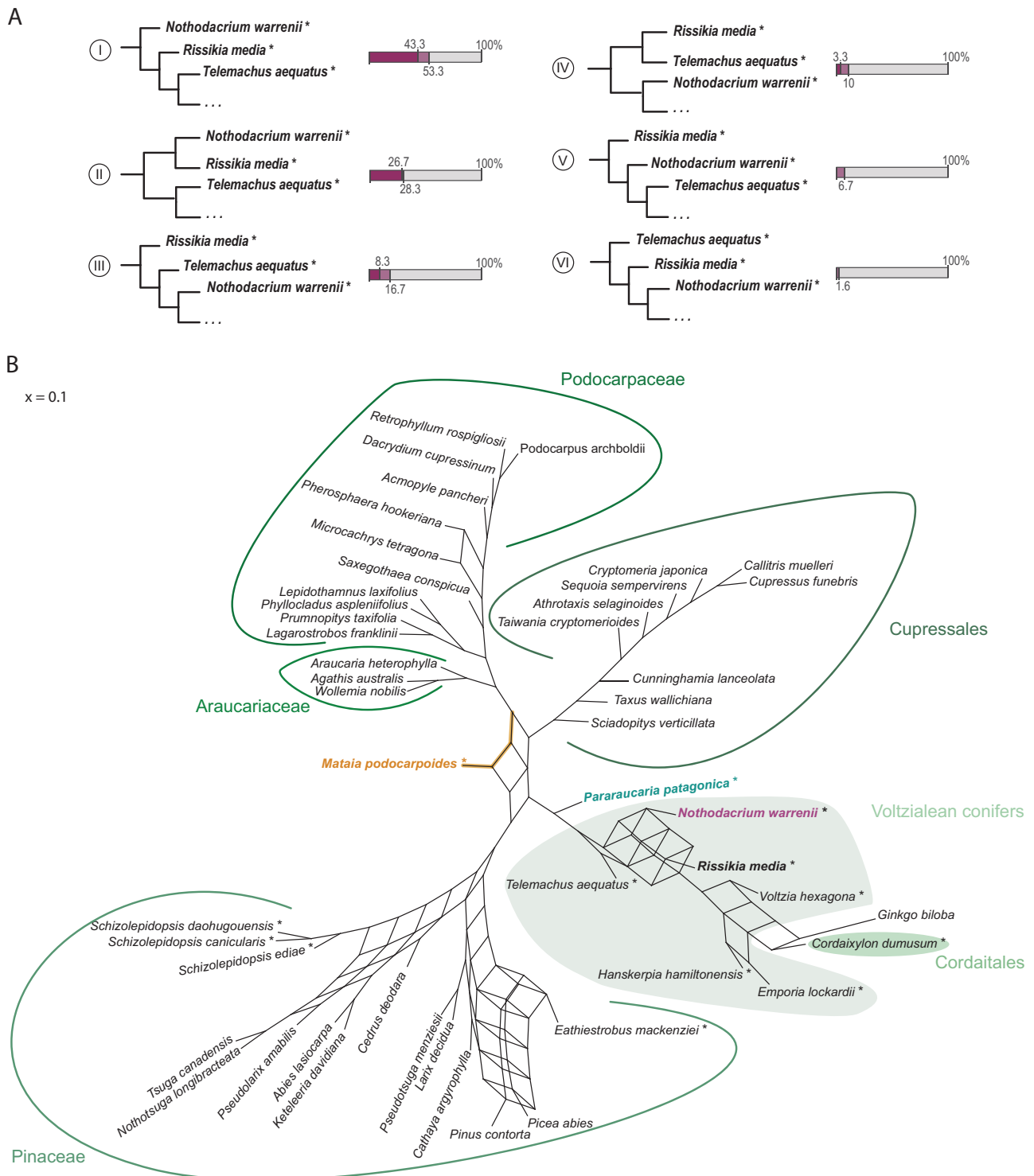


Figure 2. A, Alternative arrangements of the Voltzian conifers obtained in the maximum parsimony analyses (from most to least common), bars next to each topology indicate the percentage of analyses that recover that position in all most parsimonious trees (value above the bar) and in at least some of the most parsimonious trees (value below the bar; see explanation in Fig. 1 caption). B, Consensus network with a 10% cut-off of the most parsimonious trees obtained in 30 analyses. The orange line indicates the most common position of *Mataia podocarpoides*.

weighted analyses resulted in an unstable positioning of *Mataia*, either as sister to Araucariales (Fig. 1 orange full line), to the total group of Pinaceae, or to crown group conifers or Cupressales (Fig. 1). All analyses performed under extended implied weights with high weighting force ($k = 3$) resulted in positioning of

Mataia as sister to total group Pinaceae (Fig. 1 orange dotted line; Summary Table, Supporting Information, Appendix S4).

Nothodacrium and *Rissikia* were recovered in all most parsimonious trees in the conifer stem group, a region of the tree populated by voltzian conifers. The relationships among

the voltzialean taxa are variable (Summary Table, [Supporting Information, Appendix S4](#); [Figs 1, 2A](#)).

Pararaucaria was recovered as sister to the crown group of conifers in 91.7% of analyses as the single most parsimonious position and in all analyses at least as one of the most parsimonious positions ([Fig. 1](#) turquoise full line; Summary Table, [Supporting Information, Appendix S4](#)). Under equal weights and no monophyly constrain within Pinaceae, *Pararaucaria* is recovered as sister to crown conifers or to Araucariales ([Fig. 1](#) turquoise dotted line; Summary Table, [Supporting Information, Appendix S4](#)).

The *Schizolepidopsis* species form a clade commonly placed as sister to crown group Pinaceae ([Fig. 1](#) grey full line), and in some analyses in variable positions within Pinaceae ([Fig. 1](#) grey dotted line).

Bayesian analysis

The Bayesian analysis recovered the Cordaitalean *Cordaixylon*, and the voltzialean *Emporia* and *Hanskerpia* forming a clade ([Fig. 3A](#)), rather than as successive sister taxa to the total group of conifers as observed in the parsimony analyses results ([Fig. 1](#)). *Nothodacrium* and *Rissikia* are recovered as sister taxa, as in most parsimony analyses that included the discrete version of the character describing the number of ovuliferous complexes per cone (character 66; [Figs 1](#) purple dotted line, [3A](#)), which was the character version used in the Bayesian analysis. *Mataia* is recovered as sister to total group Pinaceae, and *Schizolepidopsis* is found as polyphyletic with *S. longipetiolus*, *S. canicularis*, and *S. daohugouensis* as part of stem group Pinaceae, and *S. ediae* as part of its crown group ([Fig. 3A](#)). *Telemachus* is found as sister to Cupressales, and *Pararaucaria* as sister to Araucariales ([Fig. 3A](#)). Deep nodes associated with fossil taxa, as well as some internal nodes within Pinaceae, show low posterior probabilities that likely reflect instability of fossil taxa ([Fig. 3B](#)).

Diversity curves

Diversity curves show few fossil genera in the Jurassic, which represent occurrences from Europe and South America ([Figs 4, 5](#)). There is an increase in number of genera by the Lower Cretaceous ([Fig. 4](#)), partially explained by two prolific fossil sites: the Rajmahal Formation (India) with seven genera and 17 species, and the Anfiteatro de Ticó Formation (Argentina) with five genera and species (each genus with a single species, [Supporting Information, Table S2](#) in [Appendix S1](#)). Other localities with Lower Cretaceous records are from Oceania, Asia, Antarctica, and Europe ([Fig. 5](#); [Supporting Information, Table S2](#) in [Appendix S1](#)). Since the Upper Cretaceous the Podocarpaceae fossil record is dominated by extant genera ([Fig. 4](#); [Supporting Information, Table S2](#) in [Appendix S1](#)), with most occurrences coming from Oceania, followed by South America and fewer in Antarctica, Asia, and North America ([Fig. 5](#); [Supporting Information, Table S2](#) in [Appendix S1](#)). There are apparent diversity spikes in the Early Palaeocene, Middle Eocene, Early Oligocene, and Early Miocene of Oceania, and Middle Eocene of South America ([Fig. 5](#)). The highest diversity spike of total occurrences occurs in the Middle Eocene followed by another one in the Lower Oligocene ([Fig. 5](#), grey dotted line),

coinciding with an increment in the number of extant genera reported ([Fig. 4](#)).

DISCUSSION

Morphology of extant Podocarpaceae

The main proxy for identifying extinct Podocarpaceae is the comparison with extant taxa. This is straightforward for most recent records ([Wilf 2012](#), [Wu et al. 2020](#)), but becomes challenging deeper in the fossil record because of the derived nature of many extant podocarpaceous traits. Extant Podocarpaceae exhibit wide morphological variation in their photosynthetic units ([de Laubenfels 1972](#), [Quinn 1987](#), [Brodribb 2011](#), [Farjon 2017](#)) and ovulate cones ([de Laubenfels 1972](#), [Quinn 1982](#), [Tomlinson 1992](#)). Photosynthetic organs include modified branch systems (phylloclades, *Phyllocladus*, [Tomlinson et al. 1989](#)), scale-like leaves (e.g. *Lagarostrobus*, *Halocarpus*, [Quinn 1982](#), [Wells and Hill 1989a](#)), broad multi-veined leaves (*Nageia*, [Page 1988](#)), and relatively broad single-veined leaves that are bilaterally flattened (*Acmopyle*, *Dacrycarpus*, and *Falcatifolium*; [Lee 1952](#), [de Laubenfels 1969a, b](#), [Mill et al. 2001](#)), or bifacially flattened (e.g. *Retrophyllum*, *Prumnopitys*; [Buchholz and Gray 1948](#), [Mill 2016](#)). Some genera show secondary leaf arrangements that maximize sunlight exposure. Examples are the pseudo-distichous secondary arrangement achieved by different means in different genera (e.g. *Acmopyle*, [Sahni 1920](#), *Retrophyllum*, [Mill 2016](#)), constituting complex photosynthetic units ([Brodribb and Hill 1997](#)), and the compression of the primary helical phylloclade arrangement of *Phyllocladus* into pseudo-whorls ([Andruchow-Colombo et al. 2019b](#)). The phylloclades and the expanded, bilaterally flattened leaf type are unique to Podocarpaceae, whereas the other leaf types are found in other conifer families too ([de Laubenfels 1953](#)). Broad multi-veined leaves of *Nageia* are similar to those found in *Agathis* (Araucariaceae, [Whitmore 1980](#)); relatively broad bifacially flattened single-veined leaves of genera like *Prumnopitys* and *Retrophyllum* are also found in Taxaceae and Cupressaceae ([Farjon 2017](#)); and scale-like leaves are the most common type within conifers, being present in Cupressaceae, Araucariaceae ([Farjon 2017](#)), and the extinct Cheirolepidiaceae ([Watson 1982](#)).

Epidermal characters have been described for many Podocarpaceae genera. Some features seem characteristic of certain genera, like polar subsidiary positions occupied by ordinary epidermal cells (*Falcatifolium*, *Dacrydium*, *Dacrycarpus*, [Stockey and Ko 1988](#), [1990](#), [Wells and Hill 1989a](#)) and random orientation of stomata (*Lagarostrobus*, *Manoao*, some *Lepidothamnus*, *Halocarpus*, *Parasitaxus*, [Wells and Hill 1989a](#), [Andruchow-Colombo et al. 2019a](#)), and are valuable to assess the podocarpaceous affinity of Cenozoic fossils ([Wells and Hill 1989b](#), [Carpenter et al. 2011](#), [Jordan et al. 2011](#), [Andruchow-Colombo et al. 2019a](#)). However, most epidermal characters in conifers are not restricted to single families [e.g. number of subsidiary cells, shape and arrangement of epidermal cells, Florin rings presence ([Florin 1931](#))], are variable within the same species ([Clugston et al. 2017](#)), or seem to lose signal relatively quickly in deep time (e.g. papillae are absent in Cenozoic podocarps but they are present in Early Cretaceous records, [Archangelsky and Del Fueyo 1989](#)).

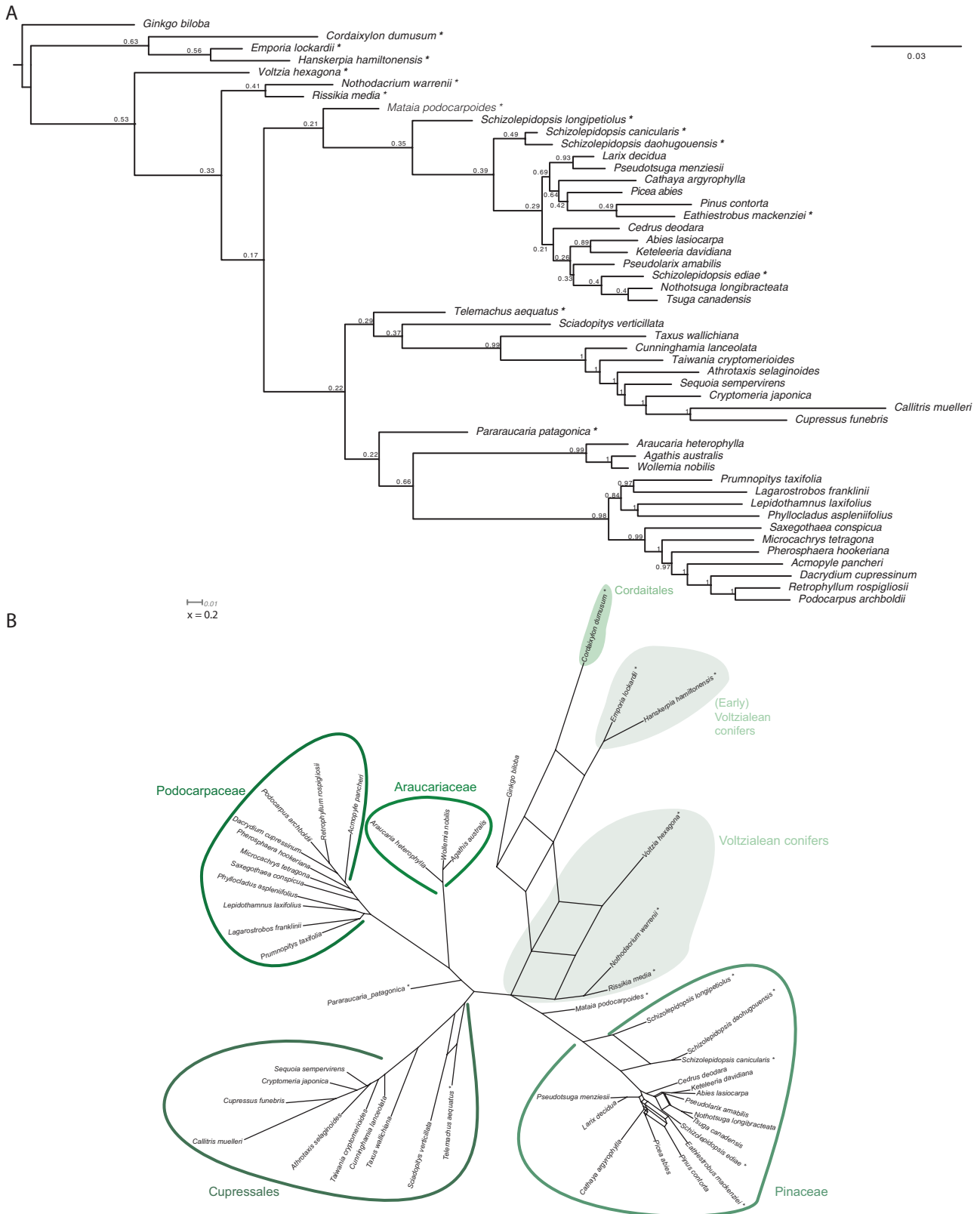


Figure 3. A, Phylogenetic relationships of *Nothodacrium*, *Rissikia*, and *Mataia* based on Bayesian total evidence analysis. All fossil taxa are indicated with an asterisk, posterior probabilities are printed next to the nodes. B, Consensus network with a 20% cut-off of the sampled trees obtained in the Bayesian analysis.

Podocarpaceae seed cones are highly variable but always show a single seed per ovuliferous complex. *Microcachrys* and *Saxegothaea* have multi-seeded cones. *Microcachrys* has fleshy seed cones with whorled ovuliferous complexes, whereas *Saxegothaea*

has coriaceous seed cones with spirally arranged ovuliferous complexes (Thomson 1909, Florin 1951, Farjon 2017). Other genera most commonly exhibit 1–2 ovuliferous complexes per cone (although some genera show wider ranges, Quinn 1982, Molloy

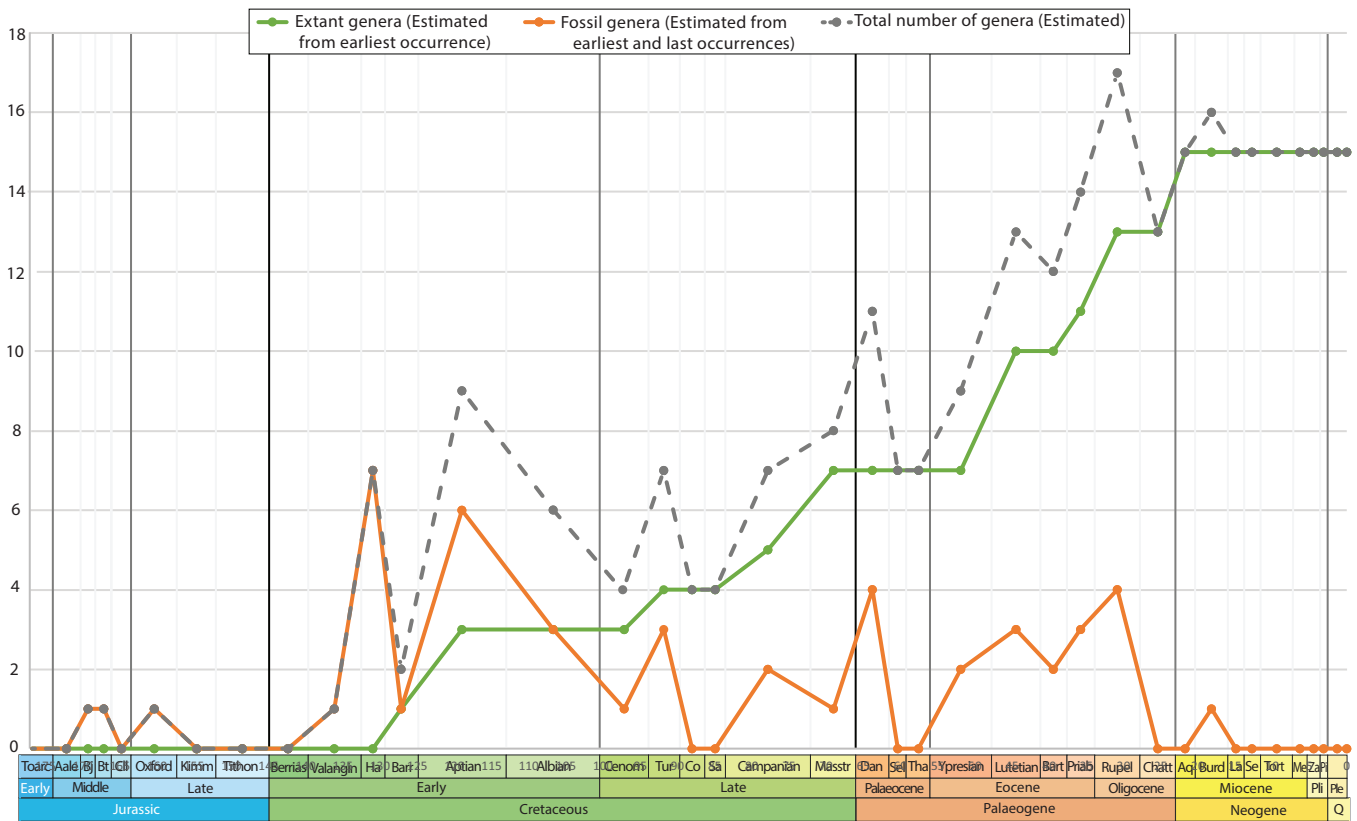


Figure 4. Curves of estimated fossil, extant, and total number of Podocarpaceae genera through time. The y-axis represents the estimated number of genera. Numbers of fossil and extant genera are estimated based on first and last occurrences ('last occurrence' of extant genera is the present). Estimated total number of genera is the sum of estimated fossil and extant genera for each time bin.

1995, Farjon 2017), show different degrees of development and fleshiness of the epimatium (from absent in *Pherosphaera* to fully covering and extending beyond the seed micropyle in *Halocarpus*, Sahni and Mitra 1927), and the presence/absence of a fleshy receptacle (Sahni and Mitra 1927, Tomlinson 1992, Mill *et al.* 2004). The epimatium is interpreted to be homologous to the conifer ovuliferous scale (Sinnott 1913, Tomlinson 1992, Englund *et al.* 2011), which is highly modified in most podocarps. It covers the mature seed partially or totally, and it can be either coriaceous, fleshy, or papery (Gibbs 1912, Sahni and Mitra 1927, de Laubenfels 1972, Molloy 1995, Farjon 2017). The receptacle (or podocarpium) is a structure resulting from the fusion of the basal, non-fertile ovuliferous complexes of the cone and sometimes the bract of the fertile complex; this structure becomes fleshy during cone maturation (del Fueyo 1999, Mill *et al.* 2001). The mature seed can be erect, oblique, or inverted, depending on the degree of development of the epimatium (Kirk 1878, Sahni 1920, Tomlinson 1992, Mill *et al.* 2001, 2004).

Podocarpaceae pollen cones are highly homogeneous and virtually undistinguishable from those of Pinaceae (Farjon 2017). They are small and have spirally arranged microsporophylls with two abaxial pollen sacs. Pollen grains are usually bisaccate (Thibout 1896, Thomson 1909, Sahni 1920, Cookson 1953, Pocknall 1981, Del Fueyo 1996), but trisaccate (Thibout 1896, Thomson 1909, Carpenter *et al.* 2011) and non-saccate (Stiles 1908) grains occur in particular genera. Non-saccate pollen also occurs in Araucariaceae (Jeffrey and Chrysler 1907, Del Fueyo *et al.* 2008), while bi-saccate pollen is common among

gymnosperms, occurring also in Pinaceae (Thibout 1896, Thomson 1909), voltzialean (Taylor and Grauvogel-Stamm 1995, Hermsen *et al.* 2007) and seed ferns (Krasilov 1977, Elgorriaga *et al.* 2019).

Fossil record of Podocarpaceae through time

Earliest (uncertain) records referred to the family

The earliest records referred to Podocarpaceae, from Permian and Triassic formations (Townrow 1967a, Blumenkemper *et al.* 2018; Supporting Information, Table S1 in Appendix S1), are here considered to have uncertain affinities with the family.

Permian: The oldest record referred to Podocarpaceae is from the Late Permian Umm Irna Formation in Jordan (Blumenkemper *et al.* 2018; Fig. 6). This fossil species was not formally described but was mentioned in a general description of the flora as a taxonomic novelty that would extend the stratigraphic range of the family (Blumenkemper *et al.* 2018). The illustrated specimen is a leafy branch with cuticle, showing helical phyllotaxy and a pseudo-distichous secondary arrangement resulting from leaf base rotation (Blumenkemper *et al.* 2018: fig. 1E-H). Leaves are lanceolate, single-veined, and have longitudinally oriented stomata arranged in rows. Stomata exhibit well-defined lateral subsidiary cells, but polar positions are seemingly occupied by ordinary epidermal cells.

The leaf morphology and arrangement are compatible with the extant genera *Retrophyllum*, *Nageia*, and *Afrocarpus*

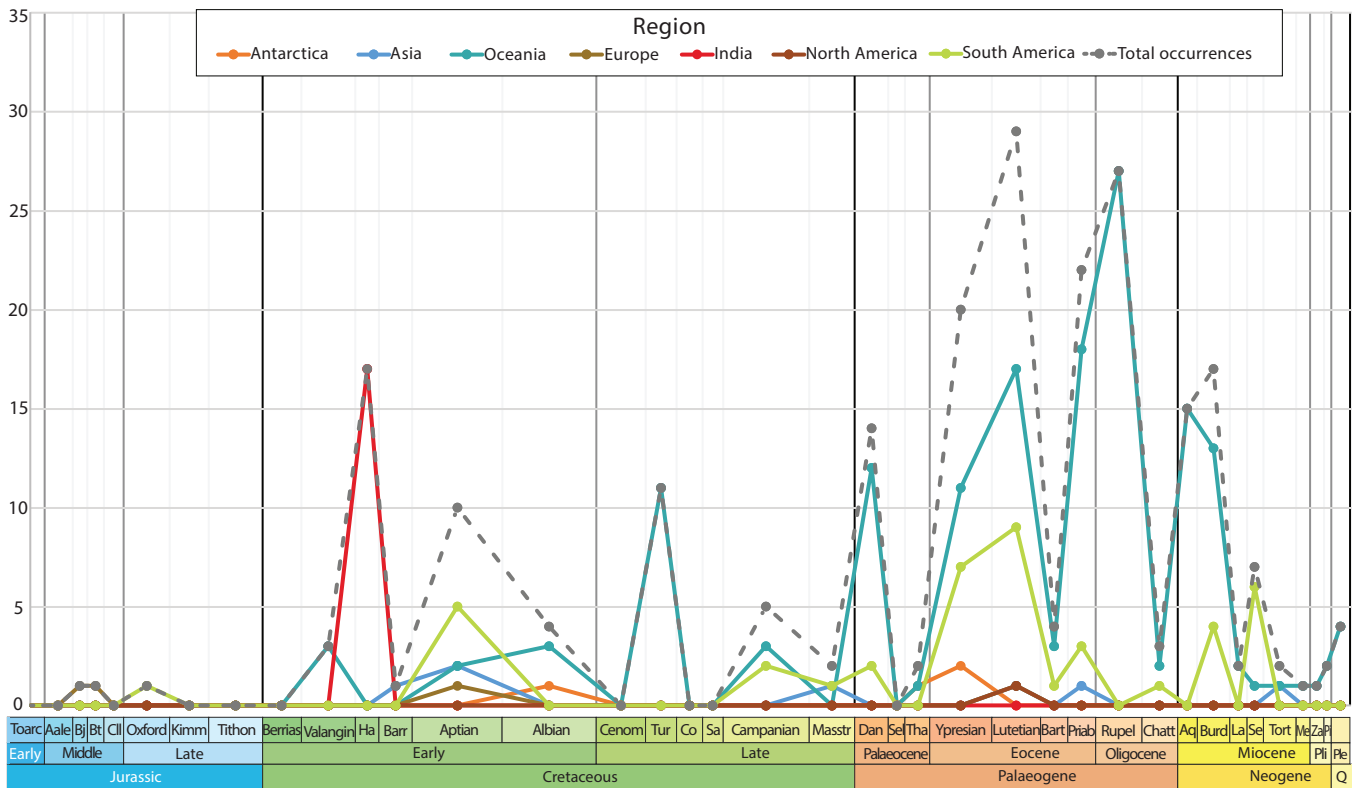


Figure 5. Observed occurrences of Podocarpaceae curves for different regions through time. The y-axis represents counts of occurrences in each time bin. Total occurrences are the sum of occurrences across all regions in each time bin.

(Knopf *et al.* 2012, Farjon 2017), whereas epidermal characters are similar to those of *Dacrycarpus* and *Dacrydium* (Wells and Hill 1989a, Stockey and Ko 1990). However, the morphology and leaf arrangement of the Jordanian taxon are not exclusive of Podocarpaceae, being found also in extant and fossil Cupressaceae and Taxaceae (de Laubenfels 1953, Taylor *et al.* 2009, Farjon 2017). Moreover, epidermal morphology seems to be variable among Mesozoic Podocarpaceae and sometimes discordant with extant and extinct Cenozoic podocarps (e.g. Harris 1979, Archangelsky and Del Fueyo 1989, Wells and Hill 1989a, b, Clugston *et al.* 2017). Therefore, the similarities in epidermal morphology between extant Podocarpaceae genera and the Permian taxon might be due to convergence rather than homology. Leaf macromorphological characters are highly variable (de Laubenfels 1953), particularly in deep time (e.g. Axsmith *et al.* 1998, Escapa *et al.* 2010, Bomfleur *et al.* 2013). Moreover, the leaf type of the Jordanian taxon is not compatible with other early records of the family (see following sections), and it is not found in the unequivocal fossil record of the family until the Early Cretaceous (Archangelsky 1966). In this context, until more leaf characters or organs of this Permian plant are known, we consider its affinity with Podocarpaceae to be dubious.

Furthermore, the region inhabited by the Permian taxon was reconstructed as an equatorial coastal lowland with a hot, subhumid climate with pronounced dry seasons (Blomenkemper *et al.* 2018), while extant and fossil broad-leaved podocarps are associated with humid climates, due to a drought intolerance related to leaf anatomical constraints (Brodrribb and Holbrook 2005, Brodrribb 2011, Wilf *et al.* 2017).

Triassic: The Triassic record of Podocarpaceae is restricted to the genus *Rissikia* (Townrow 1967a) and the associated organ-genera *Rissikianthus* (pollen cones) and *Rissikistrobus* (ovulate cones) (Supporting Information, Table S1 in Appendix S1; Fig. 6), hereafter the *Rissikia* plant. *Rissikia* is based on impressions and compressions of leafy branches with leaves that are rhomboidal in cross section to bilaterally flattened (Supporting Information, Table S1 in Appendix S1). Anderson and Anderson (2003) imply that *Rissikia* leaves are bifacially flattened with leaf bases with homofacial torsion instead. This interpretation disagrees with all other species referred to *Rissikia* (Supporting Information, Table S1 in Appendix S1) and with the original diagnosis (still valid; Townrow 1967a). The *Rissikia* leaf morphology is found in Podocarpaceae, Cupressaceae, and Araucariaceae (de Laubenfels 1953, Taylor *et al.* 2009, Farjon 2017) and has also been reported for voltzialeans (du Toit 1927, Florin 1940a).

Rissikianthus pollen cones are cylindrical with numerous helically arranged microsporophylls bearing two pollen sacs with bisaccate pollen (Townrow 1967a, Anderson and Anderson 2003). The pollen cone and pollen of *Rissikianthus* are compatible with Podocarpaceae and Pinaceae (Ting 1965, Farjon 2017, Khan *et al.* 2018). Bisaccate pollen is also characteristic of voltzialean conifers (Taylor and Grauvogel-Stamm 1995, Hermsen *et al.* 2007), and it is common among other gymnosperm groups (Krasilov 1977, Elgorriaga *et al.* 2019). Due to the extended systematic distribution and its antiquity in the fossil record, the bisaccate pollen type is either the ancestral/plesiomorphic morphology of the conifers or a highly

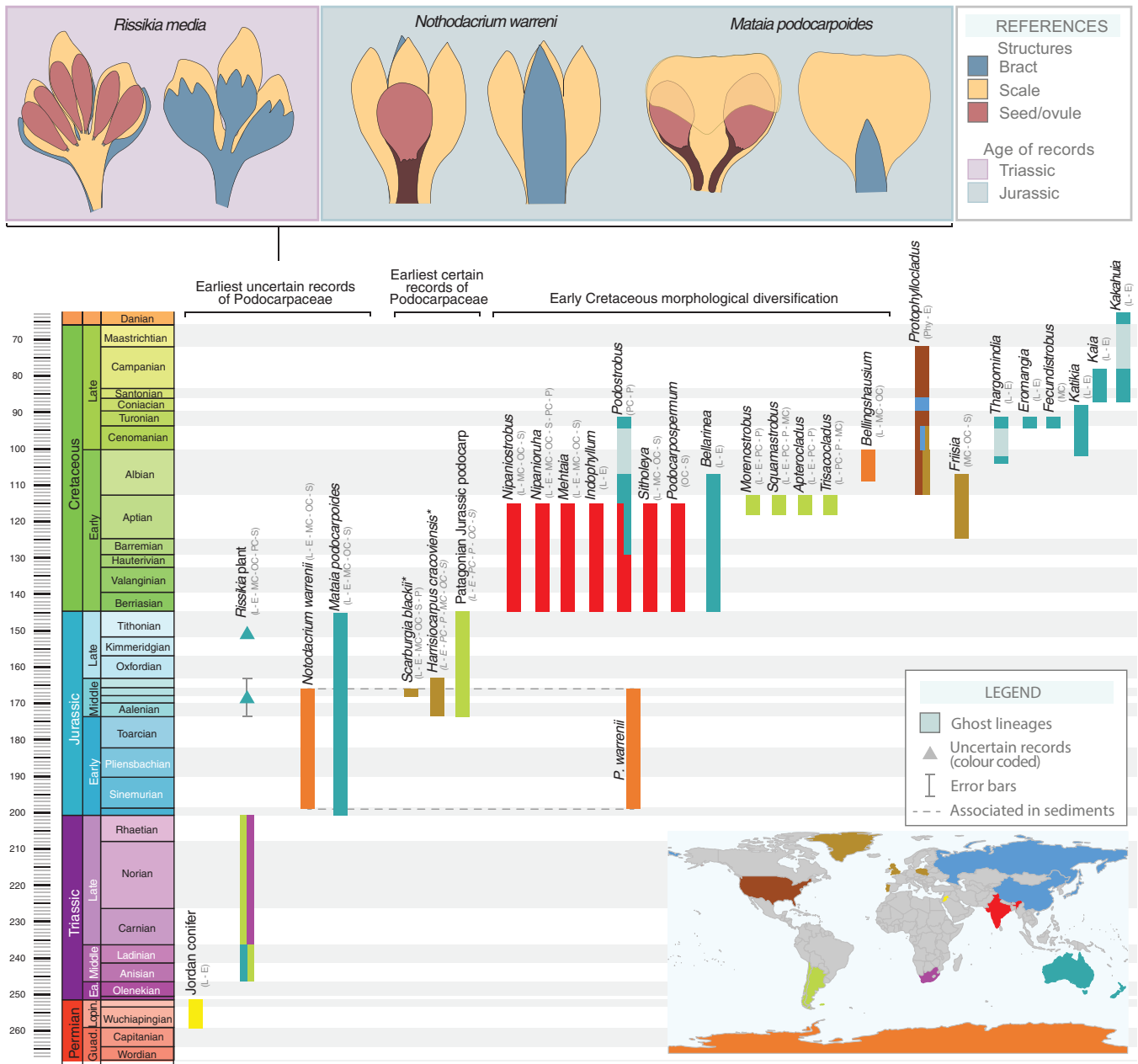


Figure 6. Biochrons (stratigraphic ranges) of fossil genera referred to Podocarpaceae from the Permian and Mesozoic. Earliest uncertain and certain records and records comprising the Early Cretaceous morphological diversification are indicated above. Colour coding of the biochron bars indicate either the provenance of the record or if it is a ghost lineage (see legend and map in the figure). Triangles (also colour coded by region) indicate uncertain records referred to the different genera. Structures described for each taxon are indicated next to the name of each genus: (E) epidermal characters, (L) leaves/leafy shoots, (MC) megasporangiate (ovulate) cones, (OC) ovuliferous complexes, (P) pollen, (PC) pollen cones, (Phy) phylloclades, (S) seeds. Diagrams of the ovuliferous complexes of three uncertain records referred to Podocarpaceae from the Triassic (light purple box) and Jurassic (light blue box) are shown.

homoplastic feature, and therefore it does not alone hold a high systematic value.

The Triassic ovulate cones referred to *Rissikistrobus* have multiple ovuliferous complexes arranged in a lax helix on the cone (Townrow 1967a, Anderson and Anderson 2003), consisting of a trilobate bract subtending a trilobate ovuliferous scale. Each scale lobe bears one to two inverted seeds (three to six seeds per ovuliferous complex). This morphology is incompatible with extant and fossil Podocarpaceae and with its sister group Araucariaceae, which have one ovule per ovuliferous complex,

but is consistent with extinct voltzialean conifers (e.g. Kerp and Clement-Westerhof 1991, Taylor *et al.* 2009). Notably, Du Toit (1927) described ovulate organs under the name *Voltzia liebiana* from the original formation of the *Rissikia* plant. Townrow (1967a: p. 113) considered these specimens nearly identical to *Rissikia*, highlighting similarities with voltzialeans. Other studies questioned the relationship between *Rissikia* and Podocarpaceae (Johnston *et al.* 1987, Leslie *et al.* 2012: supplemental material, p.25) or noted its similarities with voltzialeans (e.g. Miller 1977, Johnston *et al.* 1987).

We consider the placement of the *Rissikia* plant in Podocarpaceae to be unsupported because it is based on characters with low systematic value in deep time, and is further contradicted by characters of high systematic value. Characters of low systematic value include those demonstrated to be highly variable, like leaf and epidermal traits (de Laubenfels 1953, Miller 1977, Clugston *et al.* 2017), and those that either represent parallelisms between phylogenetically distant families (Podocarpaceae and Pinaceae) or are plesiomorphic for larger clades (conifers as a whole), such as pollen cone morphology and bisaccate pollen (Johnston *et al.* 1987). In contrast, ovulate cone characters are considered to have high systematic value in conifers (Miller 1988, Rothwell *et al.* 2009, Spencer *et al.* 2015, Andruchow-Colombo *et al.* 2018), and contradict the podocarpaceous affinities of the *Rissikia* plant (Figs 1, 3). Specifically, the ovulate cone, *Rissikistrobus*, has multiple (up to six) seeds per ovuliferous complex, unlike all members of the Araucariales (Araucariaceae + Podocarpaceae), which consistently have one. Likewise, the lobate bract and scale in *Rissikistrobus* does not occur in extant or fossil Podocarpaceae, but is common in voltzialean conifers (Florin 1951, 1954, Herrera *et al.* 2015; Fig. 1).

Further corroborating the exclusion of the *Rissikia* plant from Podocarpaceae, our phylogenetic analyses recover the *Rissikia* plant outside the conifer crown group, in an area of the phylogeny dominated by voltzialeans (Figs 1, 3).

The *Rissikia* plant is a common component of Triassic floras of the Southern Hemisphere, and due to its association with Podocarpaceae, the family is frequently cited as a component of these palaeoecosystems (see Supporting Information, Table S1 in Appendix S1). Moreover, *Rissikia* is sometimes used as a stem node calibration for Podocarpaceae in divergence time analyses (see subsection B of the discussion). Based on our analyses, we suggest that any conclusions that rely on the *Rissikia* plant's relationship to Podocarpaceae should be revisited.

Earliest certain records referred to Podocarpaceae

Jurassic records referred to Podocarpaceae are more diverse than Triassic ones, and while some of them have uncertain affinities with the family, others exhibit clear podocarpaceous morphology in all preserved organs and thus represent the earliest reliable records of the family.

Jurassic: The Jurassic record referred to Podocarpaceae comes from both hemispheres (Supporting Information, Tables S1, S2 in Appendix S1), a pattern that is also observed in its sister family, Araucariaceae (Stockey 1982, 1994, Escapa and Catalano 2013). Unlike Araucariaceae, the Jurassic record of Podocarpaceae is scarce and encompasses many taxa of uncertain affinity (Fig. 6). As with the Triassic records addressed above, these uncertain affinities are based on characters of low systematic value from leaves and pollen cones, which in several cases conflict with affinities based on ovulate cone traits (Supporting Information, Table S2 in Appendix S1). We will first address the uncertain records, and then discuss those we consider to be reliable evidence of Jurassic Podocarpaceae.

The species *Nothodacrium warrenii* (Townrow 1967b; Supporting Information, Table S2 in Appendix S1) is based on leafy branches with preserved cuticles and connected ovulate

cones. The species was found in association with *Podostrobus warrenii* pollen cones and pollen (Townrow 1967b), which are compatible with Podocarpaceae. *Nothodacrium* leaves range from scale-like to acicular and rhomboidal in cross-section, which occur in multiple extant conifer families (de Laubenfels 1953), including Podocarpaceae. The ovulate cones of *N. warrenii* bear multiple helically arranged ovuliferous complexes, which have a bract and an axillary trilobate scale bearing, but not covering, a single seed that is apparently inverted (Townrow 1967b). These characters are only partially compatible with Podocarpaceae. The seed inversion in Podocarpaceae is directly related to the degree of development of the ovuliferous scale (epimatium): inverted seeds are completely covered by it, whereas erect seeds are subtended by a reduced or absent epimatium (Tomlinson *et al.* 1991, Tomlinson 1992, Englund *et al.* 2011). Conversely, *Nothodacrium* seeds are inverted but not covered by the scale. The lobed scale of *Nothodacrium* also contrasts with the non-lobed morphology of the epimatium of Podocarpaceae species. In our phylogenetic analyses *N. warrenii* is always recovered outside of the crown group of conifers, in a region dominated by voltzialean conifers (Figs 1, 2A, 3), suggesting that this fossil plant should not be considered a member of Podocarpaceae.

The genus *Mataia* has relatively expanded, bifacially flattened leaves with helical phyllotaxis and a secondary nearly pseudo-distichous arrangement resulting from leaf base torsion (Townrow 1967a). The ovulate cones of *Mataia* are lax with multiple helically arranged ovuliferous complexes, each comprising a bract and a scale, which partially covers two inverted seeds (Townrow 1967a). Although the presence of inverted seeds enclosed in the ovuliferous scale is a trait common of Araucariales, the presence of two seeds per ovuliferous complex is not. Most of our parsimony analyses recover *Mataia* as sister to the order Araucariales (Fig. 1 orange full line). However, *Mataia* was alternately positioned as sister to the total group of Pinaceae in the Bayesian analysis and some parsimony search conditions, and in a few rare cases as sister to either Cupressales or the crown group of conifers (Fig. 1). Although the position of *Mataia* within conifers remains uncertain, these results do not support its placement in Podocarpaceae, but suggest possible affinities with Araucariales. Owing to the interesting combination of vegetative and reproductive characters seen in *Mataia*, incorporating information on other organs in phylogenetic analyses could help to clarify the relationships of this fossil plant.

The genus *Rissikia*, largely recognized in Triassic localities, also has a few Jurassic records (Supporting Information, Table S1 in Appendix S1). These were referred to *Rissikia talbragarensis*, from the Middle and Late Jurassic of Australia and New Zealand (Arber 1917, White 1981, Johnston *et al.* 1987, Bean 2006). This species has lax ovulate cones with *c.* 30 ovuliferous complexes arranged in whorls according to White (1981), but seeming spirally arranged in published images (White 1981: figs 26–30). Each ovuliferous complex shows a bract subtending a scale that bears a single inverted seed (White 1981), although it is uncertain whether the scale covers the seed. *Rissikia talbragarensis* and the Triassic *R. media* are similar in their leaf morphology and lax arrangement of ovuliferous complexes (Townrow 1965, White 1981). However, the leaf morphology is highly homoplastic in conifers (de Laubenfels 1953) and lax ovulate cones occur in

extant and extinct conifers (Stewart and Rothwell 1993, Farjon 2017). *Rissikia talbragarensis* differs from the Triassic species in its single seeded ovuliferous complexes and non-lobate bracts, although the latter trait is uncertain due to the poor preservation of the material. Overall, the poor preservation of this record makes its affinities either to Podocarpaceae or *Rissikia* uncertain.

The whole-plant *Scarburgia blackii* comprises the organ-species *Cyprissidium blackii* for scale-like leaves, *Pityanthus scalbiensis* for pollen cones with *in situ* pollen, and *Scarburgia hillii* ovulate cones, all from the Jurassic of Yorkshire (Harris 1979; Supporting Information, Table S2 in Appendix S1). *Scarburgia blackii* exhibits morphology compatible with Podocarpaceae in all its known organs. The ovulate cones are described as having multiple ovuliferous complexes, each with a single, inverted, rounded seed that is partially covered by the scale (or epimatium), and a nucellus forming a nucellar beak (Harris 1979). This morphology resembles that of some scale-leaved genera of Podocarpaceae like *Lepidothamnus* and *Manoao* (Molloy 1995, Andruchow-Colombo *et al.* 2019a). *Scarburgia blackii* is therefore among the oldest reliable Jurassic records of the family Podocarpaceae.

Harrisioarpus cracoviensis Reymanówna (1987), from the Jurassic of Poland, is another fossil taxon morphologically compatible with Podocarpaceae and comprises two morphospecies, *Harrisioarpus guckii* ovulate cones and *Cupressinocladus cracoviensis* leaves. Ovulate cones are similar to those of *Scarburgia blackii* (Harris 1979), but have whorled ovuliferous complexes. Leaves are scale-like and exhibit opposite decussate phyllotaxis (Reymanówna 1987). This combination of opposite decussate phyllotaxis and whorled ovuliferous complexes on the cones are observed together in the extant *Microcachrys* (Carpenter *et al.* 2011, Farjon 2017), a Tasmanian Podocarpaceae genus. Intriguingly, the divergence of *Microcachrys* from its closest relatives has been estimated close to the Jurassic–Cretaceous boundary (Leslie *et al.* 2018), which is congruent with the age of the *Harrisioarpus* plant.

Cupressinocladus is an organ taxon associated with multiple families. Records of this genus have been referred to Cheirolepidiaceae (Watson 1982, 1988, Okubo and Kimura 1991), Cupressaceae (Jin *et al.* 2017), Podocarpaceae (Reymanówna 1987), or left without family assignment due to the lack of cuticular and reproductive remains (Kimura *et al.* 1992, Kim 2009). Those referred to Cheirolepidiaceae have internal papillae in the stomatal pit and are associated with or connected to pollen cones bearing *Classopollis* pollen grains (Watson 1982, 1988). Those included within the Cupressaceae were linked to the extant genus *Cupressus* based on shared epidermal and seed cone morphology (Jin *et al.* 2017).

Despite the disparate familial affinities of fossils placed in the form genus *Cupressinocladus*, we argue that the best-supported relationships of the *Harrisioarpus cracoviensis* plant are with Podocarpaceae. Reymanówna's (1987) plant has opposite decussate leaves with epidermis lacking papillae, whorled ovuliferous complexes, each with a single seed, and bisaccate pollen found above the megaspore. Both the lack of epidermal papillae and the bisaccate pollen morphology eliminate the Cheirolepidiaceae affinity (Watson 1982). Regarding the possible affinities with Cupressaceae, (1) *Harrisioarpus* cones bear a single seed per ovuliferous complex, a feature ubiquitous in Podocarpaceae,

rare in Cupressaceae, and absent in *Cupressus* and related genera (Farjon 2017); (2) *Harrisioarpus* complexes show bracts and scales, as is typical of Podocarpaceae but not of Cupressaceae, especially *Cupressus* and related genera, which lack a differentiable bract and scale (Farjon 2017); and (3) the whorled arrangement of the ovuliferous complexes in *Harrisioarpus* differs from the decussate arrangement described for the cupressaceous *Cupressinocladus* (Jin *et al.* 2017). The combination of traits in the *Harrisioarpus cracoviensis* plant are present in extant and extinct Podocarpaceae and are incompatible with other conifer families, and therefore we consider the original assignment made by Reymanówna (1987) to be the most coherent hypothesis for this species, despite the complex taxonomy of *Cupressinocladus*.

An exceptionally preserved Jurassic hot spring chert flora in southern Patagonia, Argentina includes a wide array of microorganisms, coprolites, and vascular plants, including the conifer families Cheirolepidiaceae and Araucariaceae (García Massini *et al.* 2016). Notably, although not described as such in the paper, several imaged leafy branches and isolated ovuliferous complexes are likely to be of podocarpaceous affinity (García Massini *et al.* 2016, fig. 3 7–10). This has been corroborated by observation of these and other specimens from the locality (by I.H.E. and A.A.C.), and formal publication of these specimens as Podocarpaceae is forthcoming. Traits that support Podocarpaceae affinities include the presence of scale-like leaves arranged in a lax helix, with a single vein and two lateral bands of transfusion tissue, and erect seeds with additional tissues outside of the seed coat, consistent with the presence of an epimatium (García Massini *et al.* 2016, fig. 3 7–10). The arrangement of transfusion tissue in lateral bands is characteristic of Podocarpaceae (Hu and Yao 1981). These organs are also associated with pollen cones containing *in situ* bisaccate pollen (I.H.E. and A.A.C., personal observations). This material would constitute the oldest certain fossil record of the family from Patagonia and the Southern Hemisphere to date.

The Jurassic record of Podocarpaceae is not extensive but contains the first unambiguous records of vegetative and reproductive organs, and thus crucial data on early trait configurations. Jurassic seed cones are lax and multi-ovulate (Harris 1979, Reymanówna 1987), implying cone reduction, associated with bird dispersal, had not yet occurred (Pilger 1903, Sahni and Mitra 1927, Tomlinson 1992, Mill *et al.* 2004, Leslie *et al.* 2017). However, isolated ovuliferous complexes (Reymanówna 1987, García Massini *et al.* 2016) suggest they may have functioned as diaspores like in modern taxa (Contreras *et al.* 2017, Klaus and Matzke 2019). Ovule orientation in *Scarburgia* and *Harrisioarpus* (Harris 1979, Reymanówna 1987) suggest the relationship between epimatium development and seed orientation, documented throughout living Podocarpaceae (Tomlinson 1992, 2012), may have been established by the Jurassic. Pollen and pollen cone morphology have remained largely unchanged since the Jurassic (Harris 1979, Leslie 2011, Farjon 2017). The diversity of leaf morphologies during the Jurassic remains uncertain, but reliable records indicate only scale-like leaves were present (Harris 1979, Reymanówna 1987, García Massini *et al.* 2016). Further exploration of the Jurassic Podocarpaceae leaf record has direct implications for understanding when derived leaf types originated and the ecological role of the family in Jurassic ecosystems. This is key for identifying timing and mechanisms

that restricted some Podocarpaceae to humid climates (Brodribb and Holbrook 2005, Brodribb 2011, Biffin *et al.* 2012).

In the shadow of young girls in flower—Podocarpaceae in the age of angiosperms

The Cretaceous and Cenozoic record of Podocarpaceae is characterized by high morphological and taxonomic diversity. Increasing morphological diversity of leaves coincides in the fossil record with the expansion of flowering plants, which may have played an important role in shaping the morphology and distributions of Podocarpaceae. In this sense, expanded photosynthetic units evolved multiple times in the phylogeny of Podocarpaceae and have been related to competition for light in modern angiosperm-dominated forests (Brodribb and Hill 1997, Biffin *et al.* 2012, Knopf *et al.* 2012). These adaptations further restrict such taxa to ever-wet environments (Brodribb and Hill 1998, Brodribb and Holbrook 2005).

Cretaceous: Cretaceous Podocarpaceae are mostly restricted to Gondwanan landmasses (Figs 5, 6, 8). A few exceptions include reliable records from Europe and Asia (e.g. *Friisia lusitanica*, Portugal, Mendes and Kvaček 2020; *Podocarpus* [*Nageia*] *ryosekiensis*, Japan, Kimura *et al.* 1988), and some dubious records (e.g. *Protophyllocladus* from Russia, Greenland, and the United States, see Seward 1904, Florin 1940a, Tanai 1979, Andruchow-Colombo *et al.* 2019b; but see Nosova and Golovneva 2014). Conversely, the Gondwanan Cretaceous record is widespread, with fossils from Chile, Argentina, Antarctica, Australia, New Zealand, and India (Supporting Information, Table S2, Appendix S1). Early Cretaceous records were mostly referred to extinct genera (Fig. 4 in orange, 6), with a few species within extant genera (Fig. 4 in green, 8; e.g. *Podocarpus* [*Dacrycarpus*] *dubius*, Archangelsky 1966). Extant genera start to appear more conspicuously during the Late Cretaceous, with an increase from one to three in the Early Cretaceous to four to seven by

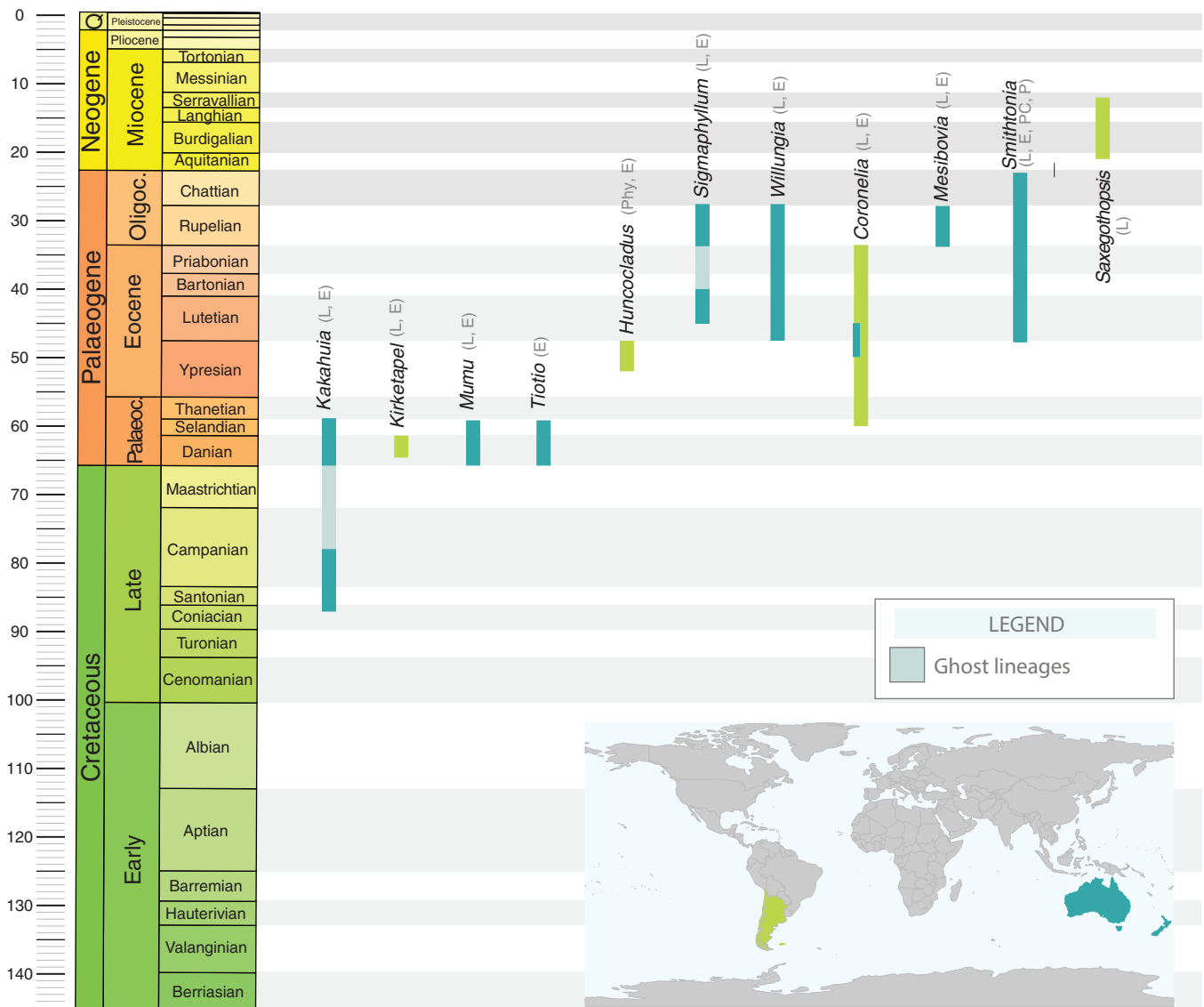


Figure 7. Biochrons (stratigraphic ranges) of fossil genera referred to Podocarpaceae from the Cenozoic. Colour coding of the biochron bars indicate either the provenance of the record or if it is a ghost lineage (see legend and map in the figure). Structures known for each taxon are indicated next to the genus name: (E), epidermal characters (L) leaves/leafy shoots, (P) pollen, (PC) pollen cones, (Phy) phylloclades.

the end of the period (Figs 4, 8; Supporting Information, Table S2 in Appendix S1; e.g. *Dacrycarpus*, Pole and Douglas 1999; *Retrophyllum*, Wilf *et al.* 2017).

Cretaceous Podocarpaceae leaves were as morphologically diverse as today. This diversity encompasses scale-like leaves (e.g. *Squamastrobis*, Archangelsky and Del Fueyo 1989), linear leaves tetragonal in cross-section (e.g. *Trisacocladius*, Archangelsky 1966), expanded, single-veined leaves that are either bifacially flattened (e.g. *Apterocladus*, Archangelsky 1966) or bilaterally flattened (e.g. *Podocarpus* [*Dacrycarpus*] *dubius*, Archangelsky 1966), and expanded multi-veined leaves (e.g. *Podocarpus* [*Nageia*] *ryosekiensis*, Kimura *et al.* 1988).

Ovulate cones are also more abundant than for previous periods, with occurrences in Argentina, India, Antarctica, Portugal, and Chile (Fig. 6; Supporting Information, Table S2 in Appendix S1). These records belong to the Early Cretaceous extinct genera *Squamastrobis*, *Trisacocladius*, *Mehtaia*, *Nipaniorua*, *Nipaniostrobus*, *Sitholeya*, *Bellingshausium*, and *Friisia* (Rao 1943, 1946, 1949, Vishnu-Mittre 1957, Archangelsky 1966, Archangelsky and Del Fueyo 1989, Cantrill and Falcon-Lang 2001, Mendes and Kvaček 2020; Supporting Information, Table S2 in Appendix S1) and to the Late Cretaceous *Podocarpus* [*Dacrycarpus*] *inopinatus* (Menéndez 1972; Supporting Information, Table S2 in Appendix S1). Most Cretaceous ovulate cones are multi-seeded and have inverted ovules, but

single-seeded cones (Vishnu-Mittre 1957, Menendez 1972) and erect ovules (*Trisacocladius*, Archangelsky 1966; *Mehtaia*, Vishnu-Mittre 1957) also occur.

In summary, the Cretaceous record of Podocarpaceae is almost entirely restricted to Gondwanan regions (Figs 5, 6). Expanded leaf types are prevalent and all extant leaf morphologies represented, which could be related to the explosive diversification of angiosperms and associated ecosystem changes (Crane *et al.* 1995, Wing and Boucher 1998, Boyce *et al.* 2010). It has been proposed that expanded leaf morphologies arose in the Early Cenozoic in response to the expansion of angiosperms in modern forests (Brodrribb and Hill 1997, Biffin *et al.* 2011, Brodrribb 2011), but the fossil record suggests that this occurred earlier, by the Early Cretaceous. Considering these morphological patterns in the fossil record of Podocarpaceae, together with the high abundance of extinct genera and incipient emergence of some modern genera (Figs 4, 6; Supporting Information, Tables S2, S3 in Appendix S1), it appears that the Cretaceous is characterized by an early diversification within the Podocarpaceae crown group, which involved expansion of morphological diversity and establishment of major clades.

Taxonomic revisions are needed for some of the Cretaceous records of this family, including new combinations for *Podocarpus inopinatus* (Menendez 1972) and *Podocarpus dubius* (Archangelsky 1966), which should be transferred to

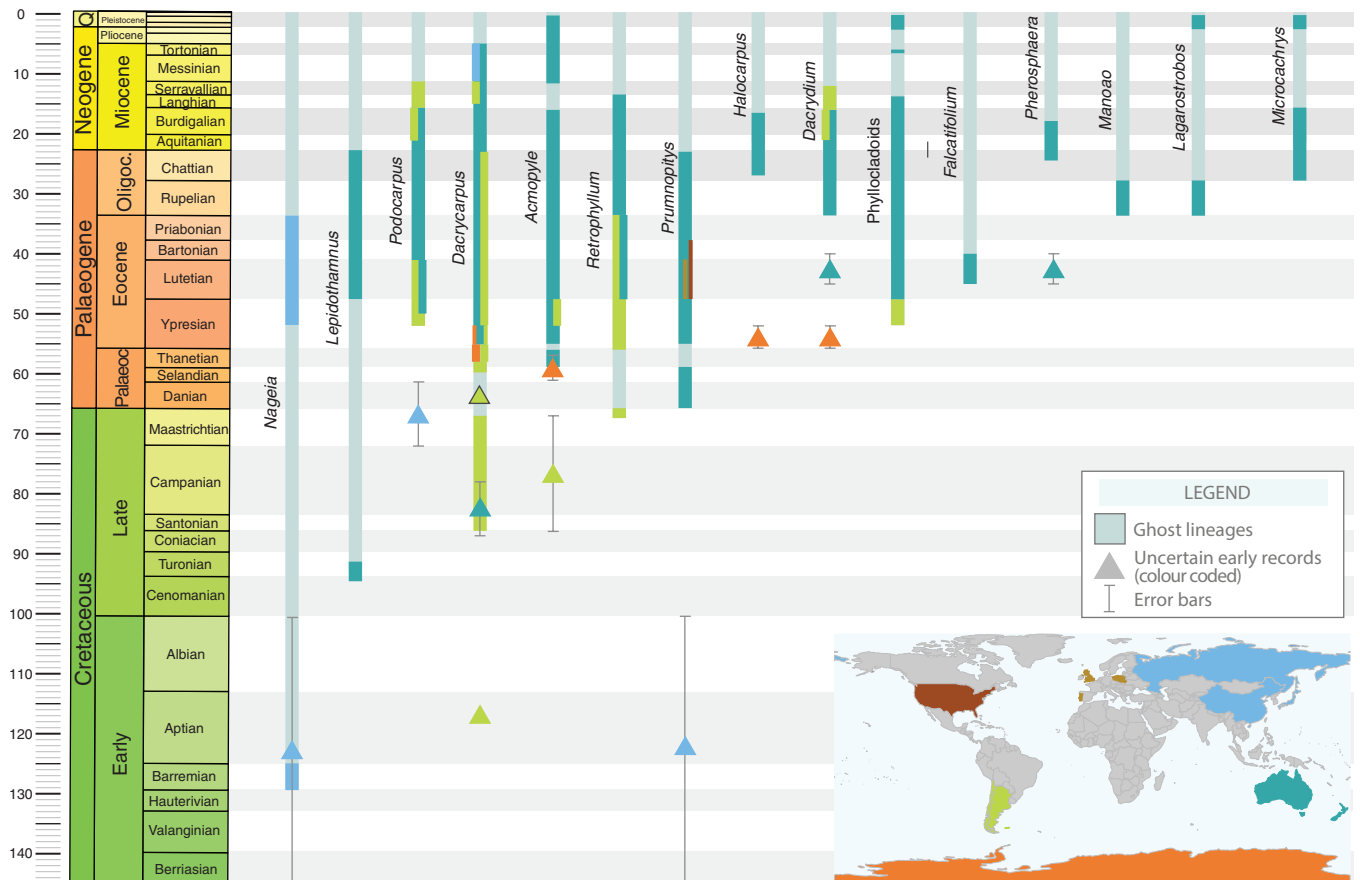


Figure 8. Biochrons (stratigraphic ranges) of extant genera referred to Podocarpaceae. Colour coding of the biochron bars indicate either the provenance of the record or if it is a ghost lineage (see references and map in the figure). Triangles (colour coded by region) indicate uncertain records referred to the different genera. Error bars indicate age uncertainty for early uncertain occurrences.

Dacrycarpus (Endl.) de Laubenfels (1969a) based on having bilaterally (rather than bifacially) flattened foliage. Likewise, *Podocarpus ryosekiensis* (Kimura *et al.* 1988) and *Podocarpus sulfunensis* (Krassilov 1965) should be transferred to *Nageia* Gaertn. based on multiveined, petiolate leaves and seed cone morphology.

Numerous Podocarpaceae fossil taxa based on exceptionally preserved ovulate cones originate from the prolific Early Cretaceous Rajmahal Formation in India (Supporting Information, Table S2 in Appendix S1; Figs 5, 6; Rao 1943, 1946, 1949, Vishnu-Mittre 1957, Banerji and Ghosh 2006, 2008, Ghosh *et al.* 2018). This formation also contains pollen cones and leafy shoots (Rao 1943, 1946, 1949, Vishnu-Mittre 1957, Rao and Bose 1970; Supporting Information, Table S2 in Appendix S1), and undoubtedly constitutes the most significant fossil locality in the world for the study of ancient podocarps.

Cenozoic: The Cenozoic fossil record of Podocarpaceae is abundant and has representatives of most extant genera, many of which were apparently more diverse and widespread in the past than today (Supporting Information, Table S3 in Appendix S1; Figs 4, 7, 8). Changes in diversity from the Early Cenozoic to the present are possibly related to ecological constraints and climate change from warmer and wetter to drier and cooler conditions during the latter part of the Cenozoic (Brodribb and Hill 2004, Dunn *et al.* 2015, Barreda *et al.* 2020), especially in regions rich in Podocarpaceae. This family is strongly associated with humid to perhumid environments (Florin 1963, de Laubenfels 1969a, b, Keng 1978, Wagstaff 2004, Farjon 2017, Kooyman *et al.* 2019; Global Biodiversity Information Facility-GBIF database, <https://www.gbif.org/>, accessed in February 2018), which were abundant in Gondwanan continents during the Early Cenozoic (e.g. Macphail *et al.* 1994, Wilf *et al.* 2005, Iglesias *et al.* 2007, Fontes and Dutra 2010, Andruchow-Colombo *et al.* in rev.). Congruently, Podocarpaceae fossils have been reported from Patagonia, Antarctica, mainland Australia, Tasmania, and New Zealand, in areas that are no longer suitable for Podocarpaceae due to Late Cenozoic aridification and glaciation (Truswell 1990, Kershaw *et al.* 1994, Macphail *et al.* 1994, Palazzesi *et al.* 2014, Dunn *et al.* 2015). Many living genera are depauperate with restricted distributions and have therefore been interpreted as relictual lineages of a historically more diverse and abundant group (Florin 1963, Farjon 2017; Supporting Information, Tables S2, S3 in Appendix S1).

The Cenozoic fossil record of Podocarpaceae comes mostly from the Southern Hemisphere (Figs 5, 7, 8), but a few occurrences were reported from the Eocene of the United States and the United Kingdom based on leaves with cuticles (Figs 5, 8; Dilcher 1969, Greenwood *et al.* 2013). Dilcher (1969) placed the North American fossil in *Podocarpus* section *Stachycarpus* subsection *Euprumnopitys*, a group that was later separated to *Prumnopitys* (de Laubenfels 1978). Further study of the North American taxon is needed, as some illustrations show that the epidermal cells of this taxon might be papillate (fig. 1D, E of Dilcher 1969), which could indicate an affinity with Taxaceae rather than Podocarpaceae (Dong *et al.* 2022). *Prumnopitys* is today distributed in New Caledonia, New Zealand, Australia, near the Andes in Patagonia, from Bolivia to West Venezuela through the Andes, and in Costa Rica (Farjon 2017). Its fossil record goes back to the Palaeocene and includes species from Australia, New

Zealand, and South America (Supporting Information, Table S3 in Appendix S1; Fig. 8). If these Northern Hemisphere fossils are indeed Podocarpaceae, their presence in the Eocene could have resulted from dispersal events from South America to North America, and then from North America to Europe.

Nageia is the only genus of Podocarpaceae with a fossil record restricted to the Northern Hemisphere, with two species from the Early Cretaceous of eastern Russia and south-west Japan (Supporting Information, Table S2 in Appendix S1; Fig. 8; Krassilov 1965, Kimura *et al.* 1988) and two from the Middle and Late Eocene of China (Supporting Information, Table S3 in Appendix S1; Fig. 8; Jin *et al.* 2010, Liu *et al.* 2015). *Nageia* has five extant species from India, southern China, Taiwan, Japan, and Mainland Southeast Asia and Malesia, while its sister genus, *Afrocarpus*, has five extant species with an eastern and southern African distribution (Farjon 2017) and no known fossil record. *Retrophyllum*, which is sister to *Afrocarpus* and *Nageia*, has a present disjunct distribution between northern South America and Australasia (Farjon 2017). The fossil record of *Retrophyllum* spans the Late Cretaceous through the Miocene of Patagonia, Australia, and New Zealand (Supporting Information, Tables S2, S3 in Appendix S1; Fig. 8). *Nageia*, *Afrocarpus*, and *Retrophyllum* form the Polypodiopsis clade, a lineage whose extant and fossil members have a biogeographic history that appears to be significantly different than that of all other Podocarpaceae lineages. Most living genera within Podocarpaceae, including *Retrophyllum*, have an extant and fossil species distribution compatible with dispersal between Australasia and South America through the Antarctic bridge (Kooyman *et al.* 2014, 2019, Farjon 2017; Supporting Information, Tables S2, S3 in Appendix S1). Conversely, the distribution of the genera of the Polypodiopsis clade suggest a dispersal event for the clade through Africa towards Asia (Supporting Information, Tables S2, S3 in Appendix S1).

Most Cenozoic species of Podocarpaceae were included in extant genera, compared with four to seven extant and 21 extinct genera in the Cretaceous (Figs 6, 8). By the Early Eocene, eight to ten extant genera were present and became widely distributed by the Mid-Late Eocene (Supporting Information, Table S3 in Appendix S1; Figs 4, 8). In the Early Miocene, 15 of the 18 extant Podocarpaceae genera were present (Supporting Information, Tables S2, S3 in Appendix S1; Figs 4, 8). Most have been identified based on macromorphology and/or epidermal morphology of vegetative structures (Supporting Information, Tables S2, S3 in Appendix S1). Many of these records show enough characters to be confidently referred to extant genera (e.g. *Microcachrys*, Carpenter *et al.* 2011; *Phyllocladus*, Hill 1989, Pole and Moore 2011; *Dacrydium*, Jordan *et al.* 2011, *Retrophyllum*, Wilf *et al.* 2017; *Acmopyle*, Andruchow-Colombo *et al.* in press.), but there are many others that require further investigation. In addition, many extinct genera occur in the Cenozoic record, corresponding to ~42% (11 of 26) of genera (Supporting Information, Tables S3, S4 in Appendix S1; Fig. 7). This diversity, both extinct and extant, supports the hypothesis that the acme of Podocarpaceae was during the Early Cenozoic, when global climatic conditions were most favourable for the ecophysiological traits that constrain them to humid environments (Macphail *et al.* 1994, Brodribb and Holbrook 2005, Wilf *et al.* 2005, Brodribb 2011, Dunn *et al.* 2015, Andruchow-Colombo *et al.* in press.).

Age of reliable records and molecular calibrations of stem Podocarpaceae

Our review and analysis of Permian to Jurassic fossils referred to Podocarpaceae indicates that many of these occurrences constitute unreliable calibrations for divergence time analyses of Podocarpaceae. Unreliable fossils that have been previously used to calibrate the stem node of Podocarpaceae include the Permian taxon from Jordan, the Triassic *Rissikia* and *Notophytum*, and the Jurassic *Mataia* and *Nothodacrium* (Biffin *et al.* 2011, 2012, Quiroga *et al.* 2015, Khan *et al.* 2022). Our study shows that the Permian taxon from Jordan, *Rissikia*, *Mataia*, and *Nothodacrium* are unlikely to be members of Podocarpaceae, whereas the Triassic *Notophytum*, originally assigned to the family (Axsmith *et al.* 1998), was later found to be part of the voltzialean *Telemachus* whole-plant concept (Escapa *et al.* 2010, Bomfleur *et al.* 2013). These fossils most likely represent stem group conifers, and therefore are not appropriate for calibrating any nodes within the conifer crown group. We therefore caution against future use of the fossil taxa as calibration points in divergence time analyses of Podocarpaceae.

Conifers with cryptic affinities and their relation to modern and transitional conifers

Our phylogenetic analyses included three widely accepted voltzialean conifers, these are *Voltzia*, *Hanskerpia*, and *Emporia* (Schweitzer 1996, Rothwell *et al.* 2005, Hernández-Castillo *et al.* 2009), as well as cryptic Mesozoic conifers with putative affinities to living lineages, these are *Telemachus*, *Pararaucaria*, and *Schizolepidopsis* (Yao *et al.* 1997, Escapa *et al.* 2010, Escapa and Leslie 2017, Matsunaga *et al.* 2021). These cryptic taxa were included to capture the broad diversity of conifer ovulate cones since their origin, and to populate stem groups of extant orders and families, thereby breaking up long branches in the conifer phylogeny. In this vein, *Telemachus*, *Pararaucaria*, and *Schizolepidopsis* are key because they combine characters of living and extinct lineages, and are therefore of especial importance for understanding the emergence of extant groups and their relationships with extinct lineages.

Our phylogenetic results differ in some respects from past analyses in the position of *Pararaucaria* and *Telemachus*, but relationships between *Schizolepidopsis* and Pinaceae remain consistent (Figs 1, 3; Matsunaga *et al.* 2021). The Triassic *Telemachus* whole plant comprises organs originally assigned to six genera from three different conifer orders, Araucariales, Cupressales, and Voltziales (Retallack 1981, Anderson and Anderson 1989, Meyer-Berthaud and Taylor 1991, Yao *et al.* 1997, Axsmith *et al.* 1998, Hermsen *et al.* 2007), but which were recently combined as part of a voltzialean whole-plant concept (Escapa *et al.* 2010, Bomfleur *et al.* 2013). All our parsimony analyses place *Telemachus* among voltzialeans (Figs 1, 2), supporting recent studies (Bomfleur *et al.* 2013). Conversely, the Bayesian analysis recovers it as stem Cupressales, although with a low posterior probability (Fig. 3), in favour with the original taxonomic assignment of the seed cone (Yao *et al.* 1997) and similar to results of Matsunaga *et al.* (2021).

Pararaucaria patagonica belongs to the extinct Mesozoic family Cheirolepidiaceae (Calder 1953, Stockey 1977, Escapa *et al.* 2012), which has been associated with Voltziales and

Araucariales, among other groups (Miller 1999, Escapa and Leslie 2017, Matsunaga *et al.* 2021). All our parsimony analyses recover *Pararaucaria* as sister to all conifers in at least some optimal trees, supporting the voltzialean hypothesis (Figs 1, 2). A few of the parsimony analyses also recovered it as sister to Araucariales (Fig. 1; see also the Summary Table in Supporting Information, Appendix S4), a position also recovered in our Bayesian analysis, albeit with a low posterior probability (Fig. 3). Although more evidence is needed to determine the placement of Cheirolepidiaceae, our analyses favour placement in the conifer stem group along with many voltzialeans. Low posterior probabilities in our Bayesian analysis are associated with the instability of the cryptic taxa *Pararaucaria*, *Telemachus*, and *Schizolepidopsis*. Examination of consensus networks at different thresholds (see Supporting Information, Appendix S7A, B) shows interaction between *Telemachus* and *Pararaucaria* in stem Araucariales and Cupressales (Fig. 3A), as well as interactions among Pinales and stem-group conifers. Some of the uncertainty in the placement of these cryptic taxa is likely due to low information content in the morphological data pertaining to the branches separating the modern conifer orders (Cupressales, Araucariales, and Pinales), and thus any particular placement is weakly supported by the data. The alternative positions of *Telemachus* and *Pararaucaria* across inferences methods, analytical conditions, and posterior trees further suggests that character conflict has a role in the overall uncertainty in the topology and low posterior probabilities (Figs 1–3, see also Supporting Information, Appendix S7).

The alternative phylogenetic placements of *Pararaucaria*, *Telemachus*, and *Schizolepidopsis* reflect the conflicting affinities previously proposed by morphology-based studies (Miller 1977, Yao *et al.* 1997, Escapa *et al.* 2010, Bomfleur *et al.* 2013, Leslie *et al.* 2013, Escapa and Leslie 2017, Matsunaga *et al.* 2021). Our dataset is currently unable to unambiguously resolve these conflicts, but the hypotheses that are favoured across analytical conditions are the voltzialean affinity of *Telemachus*, the placement of Cheirolepidiaceae in the conifer stem group, and *Schizolepidopsis* as stem-group Pinaceae. Better understanding of the placement of these taxa will require broader taxon, organ, and character sampling that resolve character conflict and provide greater information on deep nodes of the conifer crown group.

The pattern observed in the fossil record of Podocarpaceae, in which the reliable fossil record starts in the Jurassic with uncertain records trailing into the Triassic, or even Permian, also occurs in other conifer families (Stockey 1975, Kunzmann 2007, Escapa *et al.* 2008, Rothwell *et al.* 2012, Spencer *et al.* 2015, Matsunaga *et al.* 2021). It could be argued that some of the uncertain or ‘cryptic’ Triassic records of modern conifers exhibit intermediate morphologies between voltzialeans (e.g. Kerp and Clement-Westerhof 1991, Taylor *et al.* 2009, Herrera *et al.* 2015, 2020) and the modern-looking Jurassic conifers (e.g. Stockey 1975, Harris 1979, Escapa *et al.* 2008, Rothwell *et al.* 2012). It remains an open question whether such cryptic Triassic conifers are early (stem) representatives of extant families and orders, in which defining traits of their crown groups had not yet arisen. In this context, continued study and reinvestigation of poorly known cryptic taxa remain critical to understanding the origins of modern conifer diversity. Enriching the sampling of such

cryptic taxa in phylogenetic analyses is challenging but promises great reward for its contribution towards resolving the phylogeny of living and extinct conifers.

CONCLUSIONS

The study of Podocarpaceae evolution presents unique challenges due to high morphological diversity as well as a fragmentary, and sometimes ambiguous, fossil record. With this study we aimed to understand the extent to which Podocarpaceae is recognizable in deep time and to reconstruct major patterns in their evolutionary history. To do so we reviewed the fossil record of Podocarpaceae and discussed the validity of its oldest records.

We refute the affinities of Permian, Triassic, and some Jurassic records to Podocarpaceae. A Permian conifer recently described from Jordan as the earliest member of Podocarpaceae is here argued to be dubious due to the presence of derived features that do not appear in the reliable record of the family until the Early Cretaceous. The Triassic *Rissikia*, and the Jurassic *Nothodacrium* and *Mataia* are here excluded from Podocarpaceae based on careful consideration of characters and on multiple phylogenetic analyses, which included all major extant and extinct conifer groups and a wide variety of conditions. In these analyses, *Rissikia* and *Nothodacrium* are always recovered as Voltziales, whereas *Mataia* was most commonly recovered as stem Araucariales. We also discussed the phylogenetic positions of *Pararaucaria* (Cheirolepidiaceae) and *Telemachus* (Voltziales), both most frequently recovered in the conifer stem group.

The study of the diversity and distribution of Podocarpaceae through time shows that its earliest reliable records come from the Jurassic of both hemispheres. All extant Podocarpaceae leaf morphologies appeared in the record of the family by the end of the Early Cretaceous, coeval with the explosive diversification of angiosperms. Starting in the Late Cretaceous there were more extant than extinct genera reported in the Podocarpaceae fossil record and the family showed further restriction to Gondwanan landmasses contrasting with their earlier global distribution. The restriction to southern lands became more evident during the Cenozoic. In the Cenozoic, the family was most diverse during the Eocene–Oligocene with a drop in the macrofossil diversity after the Mid-Late Miocene, possibly related to processes of aridification and glaciation in large portions of their distribution areas.

SUPPLEMENTARY DATA

Supplementary data is available at the *Botanical Journal of the Linnean Society* online.

Appendix S1. Tables of fossil taxa referred to Podocarpaceae. Table S1. Record of the extinct *Rissikia* and associated genera. Table S2. Jurassic and Cretaceous records referred to Podocarpaceae (excl. *Rissikia*). Table S3. Cenozoic fossil record referred to Podocarpaceae.

Appendix S2. A, Taxon sampling. B, Character list (of the morphological block of the matrix). C, Accession numbers of GenBank for the molecular blocks of the matrix. D, Scorings of number of ovuliferous complexes (OC) per cone and its logarithmic transformation.

Appendix S3. Morphological matrix in nexus and tnt format, combined matrix in tnt format.

Appendix S4. Alignments of the molecular markers used; Bayesian analysis input and output files; Parsimony analyses scripts, optimal trees, consensus, and summary of analyses conditions.

Appendix S5. Tables of diversity through time.

Appendix S6. A, Age, citation and country of formations and fossil deposits. B, Age and location of fossil taxa.

Appendix S7. Consensus networks for the Bayesian analysis calculates with threshold values of 0.19 (a – splits shown are those found in at least 19% of the posterior sample of trees) and 0.13 (b – splits shown are those found in at least 13% of the posterior sample of trees).

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AUTHOR CONTRIBUTIONS

Ana Andruchow-Colombo (Conceptualization, Data curation, Formal analysis, Writing—original draft, Writing—review & editing, Funding acquisition, Resources), Ignacio H. Escapa (Conceptualization, Resources), Lone Aagesen (Resources) and Kelly K.S. Matsunaga (Conceptualization, Formal analysis, Writing—review & editing, Resources)

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

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