

PHYLOGENETIC ANALYSIS OF ARAUCARIACEAE: INTEGRATING MOLECULES, MORPHOLOGY, AND FOSSILS

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Premise of research. Phylogenetic relationships of Araucariaceae (Coniferophyta, Araucariales) are revised on the basis of the first combined data matrix for the family.

Methodology. Taxon sampling includes 39 ingroup species (31 extant, 8 fossils) and outgroup species of all the remaining conifer families. Five fossil *Araucaria* species, one species of the genus *Araucarites*, and two species of the extinct genera *Wairarapaia* and *Emwadea* were included in the analyses. Character sampling includes 23 genomic regions (19 plastid, 2 nuclear, and 2 mitochondrial) and 62 morphological characters (52 discrete and 10 continuous). The phylogenetic analyses were conducted with equally weighted parsimony. Additionally, several analyses under different taxon- and gene-sampling regimes were analyzed for identifying the causes of the long-lasting controversies in the interrelationships of the three extant genera of Araucariaceae.

Pivotal results. Monophyletic Araucariaceae is the sister group of Podocarpaceae, forming the order Araucariales. Monophyly of *Araucaria* and *Agathis* is also strongly supported by the data. The results of both molecular and combined analyses indicate that *Wollemia* and *Agathis* form a clade (=agathioid clade) sister to *Araucaria*. Within *Araucaria*, the analyses support the monophyly of the four currently recognized sections: *Araucaria*, *Bunya*, *Intermedia*, and *Eutacta*. Results support the monophyly of living and fossil *Araucaria* (including *Araucarites*), whereas the remaining extinct genera are placed as the stem of the agathioid clade. In terms of the sensitivity analyses performed, results suggest that inconsistencies among previous results would be related to ingroup sampling.

Conclusions. By means of a combined phylogenetic analysis, we have been able to obtain a strongly supported and well-resolved phylogeny of Araucariaceae that includes both living species and fossil species for the group. This study shows the feasibility and usefulness of phylogenetic analyses that incorporate multiple sources of evidence (molecules/morphology, living/fossil species, discrete/continuous characters).

Keywords: *Agathis*, *Araucaria*, *Wollemia*, phylogeny, combined analysis, morphology, fossil record.

Online enhancements: appendix, supplementary table.

Introduction

Extant species of the conifer family Araucariaceae have a primarily Southern Hemisphere distribution. Most of the species are endemic to Australia, New Zealand, New Guinea, or New Caledonia, and just two species, *Araucaria araucana* and *Araucaria angustifolia*, are endemic to South America (Dettmann and Clifford 2005). Extant diversity of Araucariaceae includes three genera: *Araucaria* and *Agathis*, both known from the nineteenth century, and the monotypic genus *Wollemia*, discovered ~15 yr ago in New South Wales, Australia (Jones et al. 1995). Extant species of *Araucaria* have been traditionally divided in four sections, *Intermedia*, *Araucaria* (= *Columbea*), *Eutacta*, and *Bunya* (Endlicher 1847; Wilde

and Eames 1952; Stockey 1982), which have been morphologically delimited (Wilde and Eames 1952) and subsequently retrieved in molecular phylogenetic analyses (Setoguchi et al. 1998).

Araucariaceae has an extremely rich fossil record, which demonstrates that during the Mesozoic, the family had a wide distribution in both the Northern and Southern Hemispheres (Stockey 1982, 1994; Stockey and Ko 1986; Hill 1995; Del Fueyo and Archangelsky 2002; Axsmith et al. 2008). This fossil record is particularly diverse from the Early Jurassic to the Late Cretaceous, while older occurrences are less common and are often based on ambiguous identifications (Rothwell et al. 2012). Among the three living araucarian genera, *Araucaria* has the most extensive and diverse fossil record (Hill and Brodribb 1999). However, many remains assigned to *Araucaria*, in general, those preserved as impressions, have doubtful affinities with the genus and even with the family (Stockey 1982; Dettmann et al. 2012). This is particularly evident for pre-

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Jurassic isolated vegetative remains, such as isolated leaves and wood, which have numerous homoplastic features and therefore could be related to other conifer families.

Previous phylogenetic analyses in Araucariaceae were all based on molecular information exclusively. Setoguchi et al. (1998) performed a phylogenetic study including 30 species (*Wollemia nobilis*, 19 *Araucaria* spp., and 10 *Agathis* spp.) based on *rbcl* gene sequences. Other molecular phylogenetic analyses of this family were published but also with reduced taxon- and gene-sampling regimes (Gilmore and Hill 1997; Stefenon et al. 2006; Kunzmann 2007; Codrington et al. 2009; Liu et al. 2009). Despite the differences in gene and taxon sampling, these analyses agree in the monophyly of Araucariaceae and its three genera, with high support in most cases. However, a major discrepancy among the studies appears in interrelationships of the three extant genera, as the three possible relationships among them have been retrieved in different analyses (fig. 1). Gilmore and Hill (1997), Kunzmann (2007), and Liu et al. (2009) retrieved *Wollemia* as sister to *Agathis*, with *Araucaria* at the base of this clade. This hypothesis is also supported by an analysis that included representatives of all living conifer families (Stefanovic et al. 1998; Leslie et al. 2012). On the other hand, Setoguchi et al. (1998) obtained *Wollemia* as the sister group to a clade formed by *Agathis* and *Araucaria*. Finally, Codrington et al. (2009) retrieved the remaining possible topology, with *Wollemia* and *Araucaria* forming a clade sister to *Agathis*. Similar discrepancies have been obtained for the relationships among the four extant sections of *Araucaria*. In contrast to the various molecular-based analyses performed to date, there have been no comprehensive phylogenetic analyses of Araucariaceae based on morphological data, although the potential systematic value of morphology has often been discussed within the context of gymnosperm and conifer evolution (Miller 1988, 1999; Rothwell and Serbet 1994; Doyle 1996).

Several empirical and theoretical studies emphasized the importance of an extensive taxon and character sampling in order to obtain stable phylogenetic hypotheses (Graybeal 1998; Hillis 1998; Goloboff et al. 2009). Additionally, the combination of molecular and morphological information benefits from the large amount of available molecular data makes possible the inclusion of both fossils and extant species in the same analysis. Within this context, we performed phylogenetic analyses that combine the first morphological matrix for Araucariaceae and a large molecular data set. Taxon sampling includes more than the 80% of the extant species of Araucariaceae, a large number of outgroups belonging to all extant conifer families, and eight fossils from the Jurassic and Cretaceous of the Northern and Southern Hemispheres. Finally, we explored the effect of outgroup, ingroup, and character sampling on the relationships of the araucarian genera to test whether taxon- and/or gene-sampling regimes are possible causes for the disparate results obtained in previous phylogenetic studies of the Araucariaceae family.

Material and Methods

Molecular Data

The molecular data set was built including all the available DNA sequences of conifers from GenBank that can be poten-

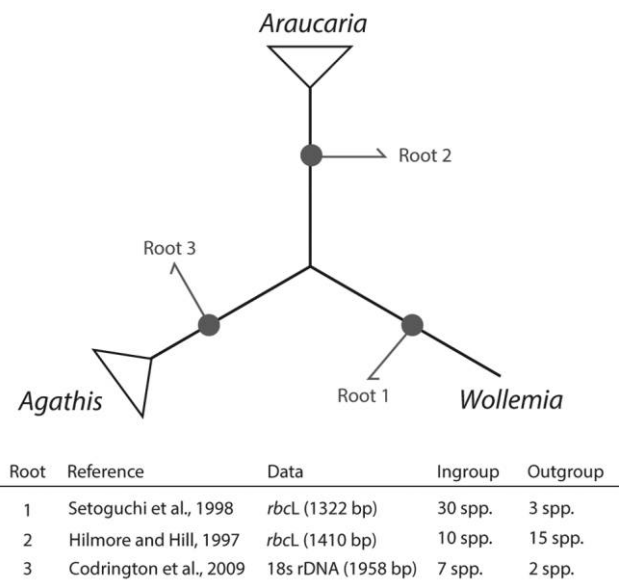


Fig. 1 Previous rooting hypotheses for Araucariaceae. One reference is included supporting each root proposal; additional references can be found in the text.

tially informative for (i) solving the relationships within Araucariaceae, (ii) testing Araucariaceae monophyly, and (iii) assessing the position of Araucariaceae within Coniferales (app. A). The data set was built with the aid of GenBank-to-TNT (Goloboff and Catalano 2012). This is a pipeline for easily creating molecular matrices, starting from GenBank files and finishing with phylogenetic matrices that can be read by the program TNT (Goloboff et al. 2008). The final molecular data set included 23 genomic regions: 19 belonging to the plastid genome (16s, *rbcl*, *matK*, *nadhF*, *nadhB*, *accD*, *atpB*, *atpF*, *nadhJ*, *psbB*, *psbD*, *psbE-psbJ*, *rpoB*, *rpl2*, *rpoC1*, *rps4*, *trnD-trnT*, *psbA-trnH*, *rps12*), two belonging to the nuclear genome (18s, 26s), and two belonging to the mitochondrial genome (*atpI*, *coxI*). Nucleotide sequences were aligned with Mafft (Katoh et al. 2005; Katoh and Toh 2008). The total number of aligned sites was 28,621. Gaps were considered missing. Data sets and resulting trees can be downloaded from <http://www.mef.org.ar/iescapa>.

Morphological Data

The morphological data set comprises 62 morphological characters (app. B, available online), scored for all the species of Araucariaceae included in the molecular data set and for 10 outgroup species (table B1, available online). Ten morphological characters represent measurements of different structures (table B1). Characters varying in a continuous scale were traditionally discretized before their inclusion in phylogenetic analyses. However, Goloboff et al. (2006) have developed a procedure for including both characters that change on a continuous scale and discrete characters (morphological and/or molecular) in a combined phylogenetic analysis. By treating continuous characters as such, the transformation cost among states is the numerical difference between the values of the

different measurements. This approach to analyzing continuous characters requires taking the scale of measurements into account; otherwise, the weight of a character may change according to the particular units of measurements (e.g., mm, cm, m). Hence, a standardization step needs to be added to the procedures. In our case, the complete range of each character was standardized as equivalent to one step of a discretely coded character (i.e., a change between the two most dissimilar states in each continuous character has the same cost as one step in a discrete character). When known, the natural variation among individuals of each taxon for a particular continuous character was scored as a range.

Character scorings were based on the study of herbarium specimens (Botany Collections of the Field Museum, Chicago; LH Bailey Hortorium, Cornell University, New York; and National Herbarium of Victoria, Melbourne, Australia) for extant species and on paleobotanical collections and specialized literature for fossil species (Colección Paleobotánica, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; Paleobotanical Collections, Natural History Museum and Biodiversity Institute, University of Kansas, Lawrence; Ohio University Paleobotanical Herbarium at the Field Museum, Chicago). The morphological matrix was assembled with the aid of Mesquite software (Maddison and Maddison 2009).

Taxon Sampling

Ingroup. The ingroup is composed of 39 araucarian species (app. A; table B1), including all the species of the type genus *Araucaria*. The data set includes eight fossil species: five of the genus *Araucaria*, *Araucarites bindrabunensis* Vishnu-Mittre from the Jurassic of Rajmahal Hills (India), *Wairarapaia mildenballii* Cantrill et Raine, and *Emwadea microcarpa* Dettmann, Clifford et Peters from the Cretaceous of Australia (Cantrill and Raine 2006; Dettmann et al. 2012). Fossil araucariaceous species included in our study (table 1) are mostly represented by isolated permineralized ovulate cones, in which morphological external features are frequently preserved together with internal anatomical details (Stockey 1975; Stockey et al. 1992; Cantrill and Raine 2006; Dettmann et al. 2012). Miller (1999) discussed the reasons for emphasizing ovulate cones in conifer phylogenetic analyses: in absence of proper whole-plant reconstructions (i.e., confirmed relationships of different isolated organs), conifer ovulate cones may constitute the structure preserving the major number of informative features. In contrast, the other commonly found conifer organs in the fossil record (microsporagiate cones, pollen, wood, and

leaves) are more limited in terms of their morphological variability (de Laubenfels 1953; Miller 1999). The lack of *Agathis* and *Wollemia* fossil species in our study is, in this context, easily explained by the lack of permineralized ovulate cones of these genera in the fossil record (Kunzmann 2007). The construction of a morphologically based phylogenetic hypothesis including fossil species preserved as impressions/compressions may require the inclusion of a higher number of continuous morphological traits, including characters describing shape variation (e.g., pollen cones in *Agathis*). Characters for additional organs were also scored for few fossil species in which the ovulate cone has been found in organic connection with other organs (e.g., *E. microcarpa*).

Outgroup. A total number of 306 species belonging to all extant conifer families (app. A) were included as outgroups in the molecular data set. We incorporated this large number of outgroups to test the monophyly of Araucariaceae and evaluate the possible effect of outgroup sampling on the resulting relationships within the family (see below). We followed the systematic treatment of Farjon (2010) for extant species-level taxonomy and that of Christenhusz et al. (2011) for supra-generic taxonomy.

Phylogenetic Analyses

In addition to the combined analysis that included all species (extant and fossils) and all data (molecular and morphological), three complementary analyses were conducted: morphological data for all the species, morphological data for extant species, and molecular data for extant species.

Phylogenetic searches were conducted in TNT (Goloboff et al. 2008), using equally weighted parsimony as an optimality criterion. The parsimony analysis departed from 50 random addition sequences (RAS) followed by tree-bisection-reconnection. The resulting trees were submitted to a combination of Ratchet (default options), Tree Drifting (default options), and Sectorial Searches (with *Exclusive*, *Constrained*, and *Random* selection for the sectors). Group support was assessed and also by absolute jackknifing frequencies with the following settings: five RAS per replicate followed by Tree Drifting and Sectorial Searches and an independent probability of character removal of 0.36 (Goloboff et al. 2003). To evaluate hypotheses of relationships that did not appear in the optimal trees, we ran constrained searches forcing the appearance of the groups of interest. The constrained searches were run using the same settings as those considered in the original searches.

Phylogenetic analyses have dramatically increased in size,

Table 1

List of Fossil Species Included in the Combined Phylogenetic Analysis

Fossil	Age	Distribution	Reference(s)
<i>Araucaria mirabilis</i>	Middle Jurassic	Argentina	Calder 1953; Stockey 1975, 1978
<i>Araucarites bindrabunensis</i>	Jurassic	India	Vishnu-Mittre 1954
<i>Araucaria sphaerocarpa</i>	Middle Jurassic	England	Stockey 1980a
<i>Araucaria brownii</i>	Late Jurassic	England	Stockey 1980b
<i>Araucaria nipponensis</i>	Late Cretaceous	Japan, Russia	Stockey et al. 1994
<i>Araucaria vulgaris</i>	Late Cretaceous	Japan	Stockey et al. 1992; Ohsawa et al. 1995
<i>Emwadea microcarpa</i>	Early Cretaceous	Australia	Dettman et al. 2012
<i>Wairarapaia mildenballii</i>	Early-Late Cretaceous	New Zealand	Cantrill and Raine 2006

and many matrices are based on data sets of multiple origins. Different approaches have been proposed in order to develop phylogenetic hypothesis from different lines of evidence (Nixon and Carpenter 1996). In the “total evidence approach” (Kluge 1989), all the available information is integrated in a simultaneous analysis in order to find the most parsimonious hypotheses (Kluge 1989; Nixon and Carpenter 1996). We agree with many different authors in considering the total evidence approach as the best approach to phylogenetic inference. In that sense, our results will be discussed following combined analyses (figs. 2–4), which are illustrated and considered the best hypothesis for all the available information. Complementarily, results of single data sets are also compared to evaluate the phylogenetic signal of the different partitions.

Evaluating Sampling Effects

In order to evaluate the causes of the discrepancy among previous phylogenetic analyses in Araucariaceae (see above), we evaluated how taxon and gene sampling affect the monophyly and interrelationships of the three extant genera of Araucariaceae. The effect of the outgroup sampling was evaluated by generating new matrices, each one including the ingroup and the species of a single conifer family as the outgroup. On

the other hand, the ingroup sampling effect was evaluated by analyzing matrices that included a reduced number of species of *Agathis* and *Araucaria* (1, 2, 5, and 10). The analyses were replicated using 100 randomly selected taxon sampling regimes for each number of ingroup species. Finally, to evaluate the effect of gene sampling on the results, we repeated the previous analyses but in this case including only *rbcL* sequences because this gene is the one with the largest number of species sequenced and one of the most commonly used in previous studies (Setoguchi et al. 1998). The sensitivity analyses described above required analyzing more than 1000 matrices. These analyses were performed in an automated way via scripts written in TNT macro language (available from the authors on request). The tree search settings were the same as for the original matrix (see above).

Results

Phylogenetic Analyses of Extant Araucariaceae

Combined data. The combined analysis included 4569 parsimony-informative molecular characters and 59 parsimony-informative morphological characters. Parsimony search of the combined matrix resulted in >1000 most par-

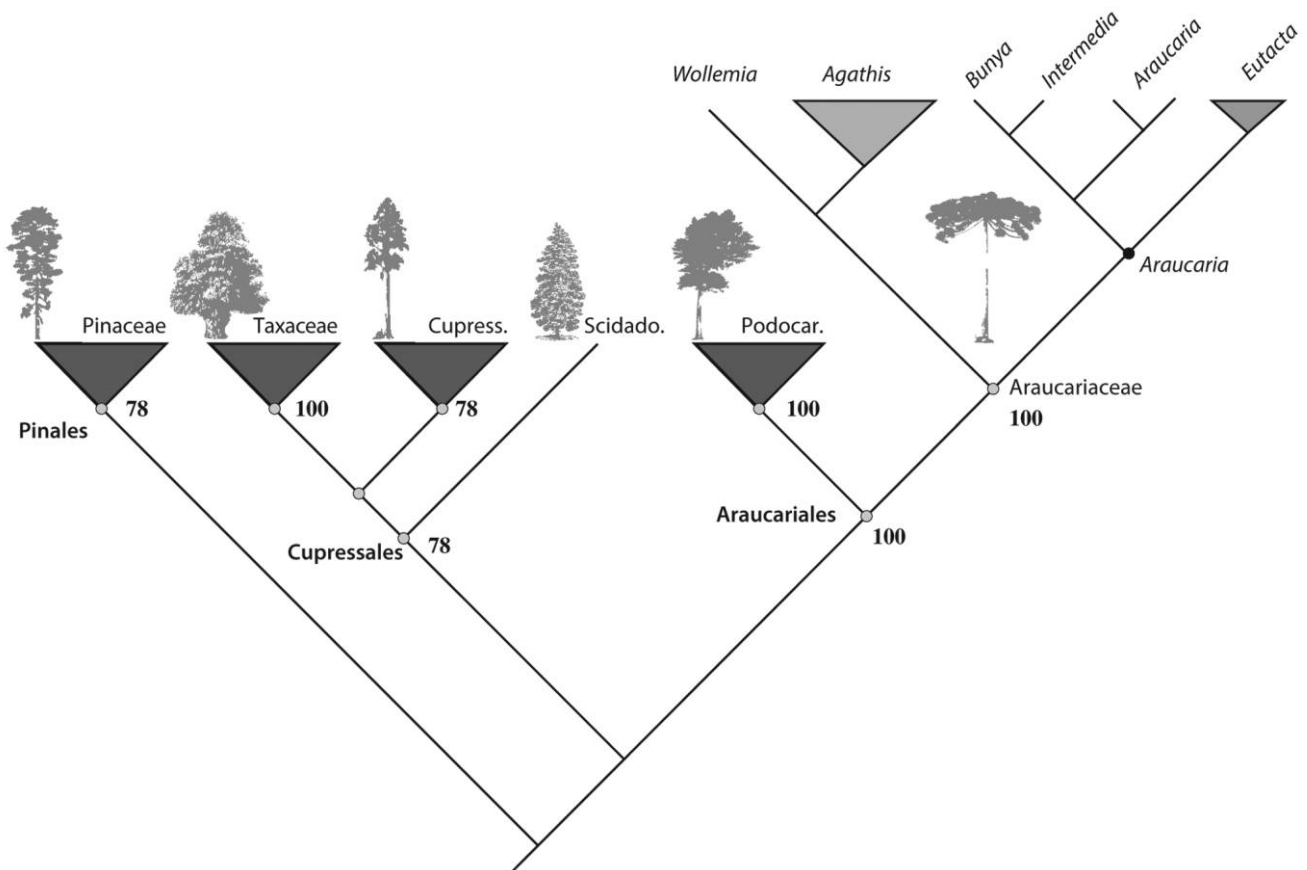


Fig. 2 General phylogenetic relationships for Araucariaceae and other conifer families supported by the combined and molecular data sets. Numbers on the nodes indicate jackknife support values for extant conifer families. Line drawings modified from Farjon (2010). Cupress. = Cupressaceae; Podocar. = Podocarpaceae; Scidado. = *Sciadopitys*.

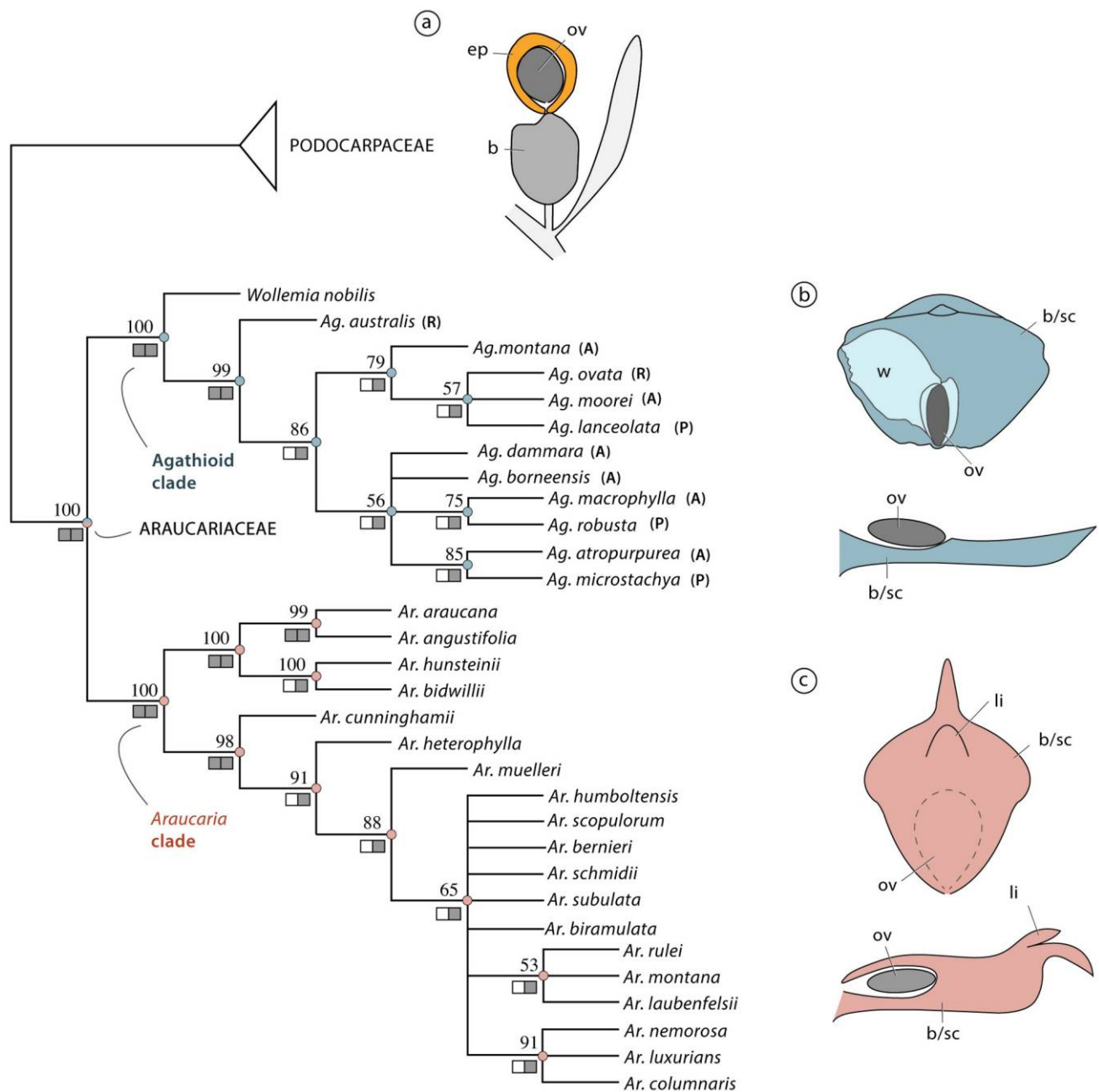


Fig. 3 Phylogenetic hypothesis among extant species of Araucariaceae obtained with the combined matrix. Numbers on the nodes indicate jackknife support values; nodes with frequencies less than 50 were collapsed. Squares below each node indicate support of molecular data set (right) and morphological data set (left) if independently analyzed (supported = gray; unsupported = white). Bold letters on the right of *Agathis* species indicate previous assignment to sections: *Agathis* (A), *Prismatobracteata* (P), *Rostrata* (R). Line drawings indicate bract/scale morphologies in Podocarpaceae (a), agathoid clade (b), *Araucaria* (c). b = bract; b/sc = bract/scale complex; ep = epimatium; li = ligule; ov = ovule; w = wing.

simonious trees (MPT) of 15,175.20 steps (figs. 3, 5). In this case, as in all the remaining analyses performed, the searches were ended after consensus stabilization. We rooted the trees in the branch leading to Pinaceae because it has been repeatedly obtained as sister of the remaining extant conifer families (Chaw et al. 1997; Stefanovic et al. 1998; Bowe et al. 2000; Quinn et al. 2002).

Molecular data. The molecular analysis included 28,621 characters (4569 parsimony informative). Parsimony analysis of the molecular matrix resulted in >1000 MPT of 15,036 steps. Phylogenetic relationships among external conifer families are defined mostly by the molecular data and therefore are identical to those obtained in the combined analysis. The topology of the strict consensus based on molecular infor-

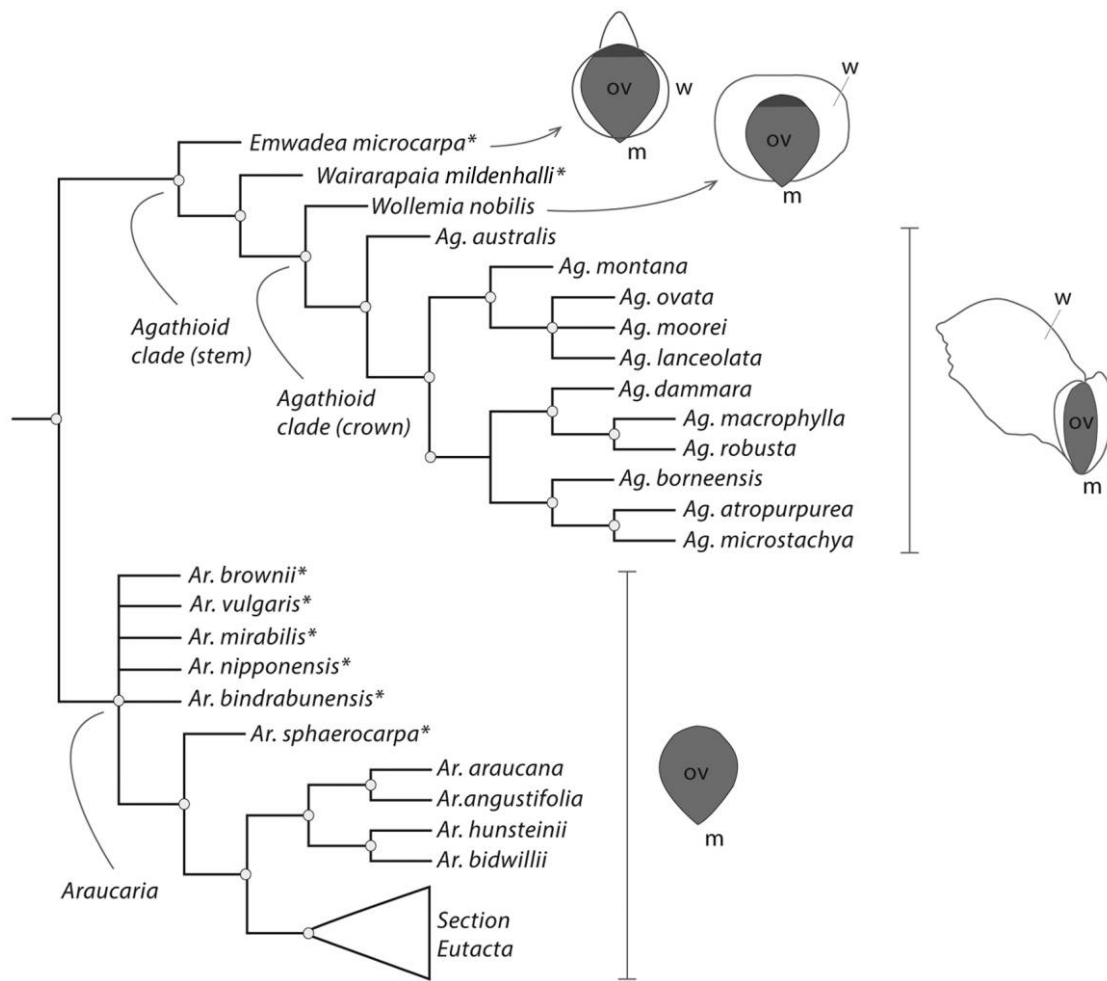


Fig. 4 Strict consensus of most parsimonious trees obtained with the combined matrix for extant and fossil Araucariaceae. Fossil species are indicated with an asterisk. Line drawings illustrate seed and seed wings (modified from Dettmann et al. 2012). m = micropyle; ov = ovule; w = wing.

mation is also congruent with the combined analysis in terms of relationships within Araucariaceae (fig. 3).

Morphological data. The morphological data set including only the extant species has 60 parsimony-informative morphological characters out of the 62 morphological characters included in the data matrix. Parsimony analysis of this matrix resulted in 22 MPT (tree length 136.6). The relationships of Araucariaceae obtained from this data set are mostly congruent with those found in both the combined and molecular analyses (fig. 3). Major points of congruence among the results of the morphological, molecular, and combined analyses are the relationships among the three extant genera of Araucariaceae and the monophyly of Araucariaceae, *Agathis*, *Araucaria*, and all nonmonospecific *Araucaria* sections (*Eutacta* and *Araucaria*). The relationships among the sections of *Araucaria* are also mostly congruent; *Araucaria* is basally split into two main clades, one including the sections *Intermedia*, *Bunya*, and *Araucaria* and the other including section *Eutacta*. However, the clade formed by *Intermedia* and *Bunya* in the results of both

the molecular and combined analyses is not supported in the morphological analysis.

Phylogenetic Analyses of Extant and Fossil Araucariaceae

Combined data. The parsimony analysis of the combined matrix in TNT resulted in >1000 MPT of 15,186.31 steps. This analysis recovered the monophyly of extant and fossil Araucariaceae, and the outgroup relationships are identical to those obtained for the analysis limited to extant species (fig. 2). *Araucaria* and *Agathis* are recovered as monophyletic, as are the *Araucaria* sections. The two recently described araucariaceous genera, *Emwadea* and *Wairarapaia*, were obtained as part of the stem of the agathiod clade (fig. 4), whereas all fossil species referred to the genera *Araucaria* and *Araucarites* cluster with extant species of *Araucaria*, forming a monophyletic group (i.e., *Araucaria*; fig. 4).

Morphological data. Parsimony analysis of the morphological matrix including extant and fossil taxa resulted in 210

MPT of 134.4 steps. As in the combined analysis, the monophyly of Araucariaceae, *Agathis*, and all *Araucaria* sections is supported by the morphological data set, indicating a high degree of congruence among different data partitions. The main differences are found in the internal relationships of *Agathis* and section *Eutacta* (fig. 4).

Sampling Influence on Araucariaceae Phylogeny

The results of the phylogenetic analyses including only one family of conifer as outgroup were identical (regarding the main relationships within Araucariaceae) to those obtained in the complete data set providing support for the monophyly of *Araucaria*, *Agathis*, and Araucariaceae, as well as for positioning *Wollemia* as sister to *Agathis*. These results suggest that in the context of our data set, the taxon sampling of outgroup taxa does not deeply affect the relationships retrieved for ingroup taxa.

In contrast, the analyses of matrices with a reduced number of ingroup taxa show a strong effect on the relative position retrieved for the three extant genera of Araucariaceae (fig. 6). In this sense, the results are more variable when the ingroup sampling is subsequently reduced (fig. 6). The sister group relationship of *Agathis* and *Wollemia*, supported by our complete analysis, is recovered in only 78% of the reduced data matrices when single species of *Araucaria* and *Agathis* were included. However, all data matrices that included at least five species of these two genera retrieved the sister group relationship of *Agathis* and *Wollemia* (fig. 6). It is interesting to note that when the taxon sampling is extremely reduced (i.e., one species per genera), the hypothesis that places *Agathis* and *Araucaria* as sister groups is recovered in 18% of the consensus trees, while trees in which *Araucaria* and *Wollemia* are sisters are never recovered. These two alternative hypotheses for ge-

neric relationships are markedly suboptimal within the context of our data set. Results of constrained tree searches indicate that trees supporting the monophyly of *Araucaria* and *Wollemia* require at least 37 extra steps and trees supporting the monophyly of *Araucaria* and *Agathis* require at least 39 extra steps.

Given that the original combined data matrix had uneven sampling among the analyzed genes, it is possible that some of the reduced data matrices resulted in taxon samplings that lack enough overlapping between the sequences of species of the three genera. If that happens, what is being evaluated is more the combination of gene and taxon sampling than the taxon sampling itself. Consequently, we performed a second round of analyses in which we analyzed how the taxon sampling affects the phylogenetic results using a single gene matrix (*rbcl*; fig. 6). In these analyses the relationships among the genera were affected in some of the reduced matrices, showing patterns similar to those obtained for the analyses with the complete gene sampling: larger effects when smaller numbers of taxa were sampled (fig. 6). The results derived from the analyses of the *rbcl* matrix are in agreement with those obtained for the complete matrix (fig. 6), suggesting that poor gene sampling was not a major cause for explaining the discrepancies among previous studies (fig. 1). These analyses altogether represent additional support for the generic relationships proposed in this article.

Discussion

Relationships of Extant Araucariaceae

The phylogenetic relationships among conifer families obtained in the simultaneous analysis and, in particular, the position of Araucariaceae as sister to Podocarpaceae are in agree-

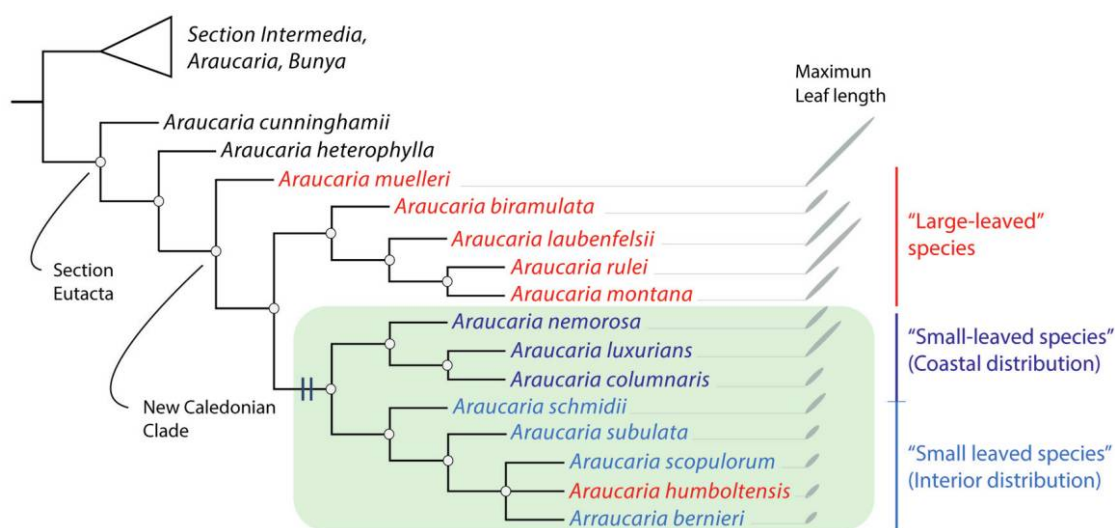


Fig. 5 Strict consensus of most parsimonious trees obtained with the combined matrix for extant species of section *Eutacta* (*Araucaria*). Species in the New Caledonian clade were color-coded following the systematic proposal of Gaudeul et al. (2012): coastal species = dark blue; small-leaved species = light blue; large-leaved species = red. Species within the green background are included in the newly defined small-leaved clade. Maximum leaf length, one of the continuous characters included in the matrix, is illustrated (gray lines) because it was considered taxonomically informative (see “Discussion”).

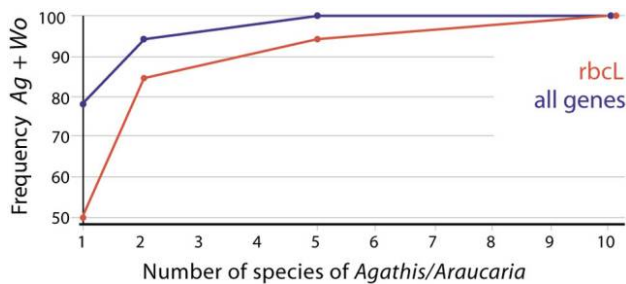


Fig. 6 Effects of ingroup sampling on Araucariaceae relationships, for the complete matrix and a submatrix exclusively based on *rbcl*. Note that frequency of the *Agathis/Wollemia* (agathioid) clade progressively increases with a higher number of ingroup species included.

ment with previous phylogenetic hypotheses for the group (Chaw et al. 1997; Stefanovic et al. 1998; Bowe et al. 2000; Magallón and Sanderson 2002; Quinn et al. 2002; Rai et al. 2008; Leslie et al. 2012) and also with the recently proposed classification of Christenhusz et al. (2011), in which Araucariaceae and Podocarpaceae belong to the order Araucariales. Today, most of its diversity is restricted to the Southern Hemisphere. Both families are extremely divergent in morphology and anatomy, which is particularly evident in the ovulate cones (de Laubenfels 1988; Farjon 2010). However, the timing and pattern in which these morphological changes occurred are mostly unknown as a result of the lack of well-reconstructed fossil species of the stem groups of Podocarpaceae and Araucariaceae or even the order Araucariales.

Araucariaceae. The monophyly of Araucariaceae, which has been previously supported by several molecular phylogenetic analyses, is here recovered analyzing the morphological, molecular, or combined data set. Strong support values for the Araucariaceae clade are provided mainly by the molecular partition, although this family is also recovered when the morphological data are analyzed alone (fig. 3). A total of six unambiguous morphological synapomorphies common to all the MPT (characters 1, 4, 5, 6, 16, 61) support the monophyly of Araucariaceae. Four of these are continuous (characters 1, 4, 5, 6), and another two are discrete characters: the presence of bract/scale complexes spreading from the ovulate cone at maturity (character 16) and the number of chromosomes (character 61). Araucariaceae also has a large number of ambiguous morphological synapomorphies. This ambiguity is explained mainly by the lack of morphological information in several outgroups (see “Material and Methods”), together with the extreme morphological divergence that exists between Araucariaceae and its sister clade Podocarpaceae. For instance, most araucariaceous bract/scale complexes are characterized by the presence of lateral extensions (character 21), which are absent in Podocarpaceae. Consequently, in order to determine the plesiomorphic state of this character (and which family has a synapomorphy for this condition), the sister group to order Araucariales must be compared and scored in the same phylogenetic analysis. If exclusively living plants are considered, the sister group of Araucariales is the order Cupressales (fig. 2), which not only is morphologically divergent with respect to Araucariales but also displays considerable internal

variability in most morphological traits (Farjon 2005) and therefore probably leads to ambiguous comparisons. A key point to solve this uncertainty would be the identification of fossil taxa placed in a basal position respecting Araucariales, which will allow determining the ancestral and derived states for bract/scale complex characters. In this context, it seems that the ability of morphological studies including only extant species is severely limited for determining the plesiomorphic and apomorphic conditions of cone characters given the large morphological gap among extant lineages. Furthermore, such a morphological gap could lead to rooting problems while evaluating the evolution of conifers using morphological data from extant species alone.

The basal split: Araucaria and the agathioid clade. The basal split of Araucariaceae leads to two strongly supported clades (fig. 3): the genus *Araucaria* and the agathioid clade formed by *Agathis* and *Wollemia*. This is in agreement with different previous molecular studies (Gilmore and Hill 1997; Kunzmann 2007; Liu et al. 2009) and in disagreement with others (Setoguchi et al. 1998). The low number of informative characters has been postulated as the main cause for the disagreements of previous phylogenetic studies (Codrington et al. 2009). It is interesting to note that, by definition, only three rooted phylogenetic hypotheses are possible to explain the relationships among three monophyletic genera and all of them have been postulated by previous studies (fig. 1). Therefore, the controversy around the relationships among living araucarian genera represents a rooting problem. This is particularly relevant since inaccurately rooted trees result in confusing evolutionary and taxonomic inferences, as well as hypotheses of character evolution (Graham et al. 2002). In this context, the sensitivity analyses here performed suggest that ingroup sampling is much more influential than other factors (outgroup selection or gene sampling) for retrieving the monophyletic agathioid clade as the sister group of *Araucaria*.

The monophyletic status of *Araucaria* is supported by three morphological unambiguous synapomorphies common to all MPT: an increase in the seed length (character 2, continuous), the absence of seed abscission (character 28), and the pinnate arrangement of the last-order branches (character 60). Additionally, the genus is also diagnosed by an ambiguous synapomorphy: the presence of thinly extended bract/scale complexes (character 22). This feature supports *Araucaria* only under accelerated transformation character optimization. The ambiguous reconstruction is explained by both homoplasy and the absence of lateral extensions in *A. araucana* and *A. angustifolia*, which result in inapplicable scorings for these taxa. On the other hand, the agathioid clade is supported by three unambiguous synapomorphies: the presence of a proximal scallop on the bract/scale complexes (character 17), the equal length in bract and scale (character 20), and the presence of integumentary wings on the seed (character 29). Additional ambiguous synapomorphies supporting the agathioid clade are explained mostly by the lack of information or/and the presence of some polymorphic conditions in *Wollemia nobilis*.

Independently of the unambiguous or ambiguous character optimization that defines the *Araucaria* and the agathioid clades, the two clades are distinct morphologically and are also strongly supported. For instance, if we consider ovulate cone features, the agathioid clade can be diagnosed as having

bract/scale complexes with a completely fused bract and scale (characters 18, 19), seeds that are adaxially disposed and nonembedded in the bract/scale complex tissues (characters 26, 32), and seeds with integumentary wings (characters 29–31) that can be symmetrical (*W. nobilis*) or asymmetrical (*Agathis* spp.). In contrast, *Araucaria* is characterized by the presence of bract/scale complexes that are incompletely fused with a free scale tip (characters 18, 19) and single unwinged seeds that are fully embedded in the bract/scale complex tissues (character 26). Additional differences between *Araucaria* and the agathiod clade are present in the leaves, microsporophylls, and tree architecture (table B1), but these features are usually highly variable within each of these clades. For instance, within *Araucaria* and *Agathis* the leaves are highly variable in terms of shape, venation, and stomata orientation (Stockey and Ko 1986; Stockey and Atkinson 1993).

The bract/scale complex tissues covering the seed(s) are a key feature that has been discussed in the context of conifer evolution (Miller 1977; Escapa et al. 2012b). The early divergence of Araucariaceae in two morphologically divergent clades has implications for testing previous hypotheses on the evolution of the bract/scale complex. The absence of seed-covering tissues in *Agathis* and *Wollemia* (fig. 3) has been repeatedly postulated as the plesiomorphic condition of Araucariaceae (Chambers et al. 1998; Setoguchi et al. 1998; Cantrell and Raine 2006). This and similar hypotheses postulated for leaves and other organs were based on a different phylogenetic hypothesis for the family, in which *Wollemia* is sister to a clade formed by *Agathis* and *Araucaria* (fig. 1). In the context of our analysis, the basal node of the agathian clade is optimized as bearing nonembedded seeds, whereas *Araucaria* is characterized by the presence of embedded seeds. Therefore, determining the plesiomorphic condition of Araucariaceae for this character requires scoring this feature in the outgroups. Podocarpaceae has been consistently considered the sister group of Araucariaceae in numerous phylogenetic analyses. Ovulate cones in most Podocarpaceae consist of one or more fertile units, each composed of a fertile bract subtending an axillary epimatium that bears a single adaxial inverted ovule. In our matrix, the podocarpaceous epimatium was postulated as homologous to the bract/scale complex tissues enclosing the seed in *Araucaria* (table B1) because it represents the most accepted theory (Tomlinson and Takaso 2002). However, the reconstruction of this character on the MPT is ambiguous for Araucariaceae, and therefore, it is not possible to support one state as derived or primitive for this character. Also, we consider that the preliminary homology hypothesis here contemplated still needs to be carefully evaluated (Tomlinson 1992).

Based on these results, some old questions remain unanswered: which is the plesiomorphic condition of the ovulate cone in Araucariaceae? What are the homology relationships between the highly modified araucariacean cones and the podocarpaceous seed cone? As discussed above, the answers to these and similar questions will need more than strongly supported multigene or morphological phylogenetic analysis of extant species; fossil taxa from the stems of Podocarpaceae and Araucariaceae will be needed in order to clarify these aspects of conifer evolution. For instance, *Pararaucaria patagonica* (Cheirolepidiaceae), from the Middle Jurassic of Ar-

gentina, has ovuliferous scale tissues that partially enclose a single seed (rarely two; Calder 1953; Stockey 1977). Interestingly, covering tissues in Cheirolepidiaceae have previously been interpreted as an epimatium (Clement-Westerhof and van Konijnenburg-van Cittert 1991; Del Fueyo et al. 2008; contra Escapa et al. 2012a, 2012b) based on the positional congruence between this ovule-enclosing tissue and the podocarpaceous epimatium. Nevertheless, phylogenetic relationships between the extinct Mesozoic family Cheirolepidiaceae and other modern conifer families (e.g., Araucariaceae, Podocarpaceae, Pinaceae) are not fully understood, and any proposed homology hypotheses for these ovulate cone traits are still quite speculative. Further studies should include this and other extinct taxa in the data matrix in order to test the potentiality to resolve the origin of some modern conifer families (e.g., Pinaceae, Araucariaceae).

The four extant sections of Araucaria. Within *Araucaria*, four sections have been classically recognized (i.e., *Intermedia*, *Bunya*, *Araucaria*, *Eutacta*), all of which have been recovered as monophyletic in the analyses of the combined, molecular, or morphological data sets (fig. 3). An early divergence event in the genus produced two main clades: one corresponding to section *Eutacta* (15 spp.) and the other including species of the sections *Bunya* (1 sp.), *Intermedia* (1 sp.), and *Araucaria* (2 spp.). The molecular information included in the combined matrix strongly supports this basal split, but the same nodes are also recovered in the morphological analysis (fig. 3). The araucarian sections were originally proposed on the basis of morphological differences (White 1947; Wilde and Eames 1952; Stockey 1982, 1994) and subsequently supported by most molecular phylogenetic analyses (Setoguchi et al. 1998). Other studies rejected some sections but with low support values (Liu et al. 2009; section *Araucaria*).

Following Farjon (2010), section *Eutacta* includes 15 species, all of which have been included in this study. This primarily New Caledonian clade is supported by five unambiguous morphological synapomorphies common to all the MPT (characters 8, 34, 41, 45, 47) in the combined analysis. The internal relationships retrieved by the molecular and combined data sets for *Eutacta* are not supported by the analysis of morphological data alone (fig. 3). As in the case of the relationships within *Agathis* (fig. 3), the morphological evidence is still insufficient for solving the relationships within this clade, and more detailed morphological character sampling must be achieved. However, one potential limitation, if a more detailed analysis is intended, is that detailed anatomical and morphological descriptions for the species of *Eutacta* are available only for some structures (e.g., leaf cuticles; Stockey and Ko 1986) or taxa, and other organs and species are still incompletely known. In the combined analysis, the internal relationships of *Eutacta* show good resolution and support (fig. 3). *Araucaria cunninghamii*, distributed mainly in New Guinea and Australia, and *Araucaria heterophylla*, distributed in Norfolk Island, are placed basally on section *Eutacta*, whereas all the New Caledonian species form a well-supported, derived monophyletic group (fig. 3). The same relationships have also been recovered by several other molecular analyses (Setoguchi et al. 1998; Stefenon et al. 2006; Gaudeul et al. 2012; contra Graham et al. 1996).

The New Caledonian clade of section *Eutacta* is often in-

terpreted as resulting from relatively recent dispersion and radiation events (Gaudeul et al. 2012). The hypothesis is supported by geological evidence that indicates New Caledonia was completely submerged during the Paleocene and Eocene (Aitchison et al. 1995). This insular clade of section *Eutacta* has extremely poor internal resolution in previous phylogenetic studies (Setoguchi et al. 1998), which has been attributed to the low divergence of the molecular markers analyzed. More recently, three monophyletic groups were defined on the basis of a phylogenetic analysis using AFLP markers (Gaudeul et al. 2012): a group including coastal species (fig. 5, dark blue), a “small-leaved species” group (fig. 5, light blue), and a “large-leaved species” group (fig. 5, red). Our analysis shows several points of agreement with this scheme: the coastal species are recovered as a monophyletic group, the small-leaved species also form a clade, but with a “large-leaved” species (*Araucaria humboldtensis*) nested within it, while the remaining four large-leaved species are clustered in a clade (i.e., *Araucaria biramulata*, *Araucaria laubenfelsii*, *Araucaria rulei*, *Araucaria montana*). Finally, *Araucaria muelleri* occupies a basal position in the New Caledonian clade (fig. 5). The main differences with previous studies are centered on the interrelationships of these groups. While in our study the coastal species are sister to the small-leaved species, in the analysis of Gaudeul et al. (2012) the small-leaved clade is sister to the large-leaved species. Interestingly, species in the coastal group have mature leaves that can be considered “small” (fig. 5), and therefore, a new “small-leaved” clade including species with coastal and internal distribution can be defined according to our results (fig. 5, green). *Araucaria humboldtensis*, which is nested in this group but was previously included in the large-leaved group, has leaves that are more similar in size to the small-leaved group (fig. 5) than to large-leaved species. Consequently, mature leaf length (character 8) and mature leaf width (character 9) are morphological unambiguous synapomorphies of the newly defined small-leaved group (fig. 5, green). In this context, it seems that continuous traits such as leaf size can be useful resolving the phylogenetic relationships of groups with recent diversification and reduced morphological divergence, where classic discrete characters may lack sufficient variation (Escapa and Pol 2011).

The clade formed by *Bunya* + *Intermedia* + *Araucaria* is supported by five unambiguous morphological synapomorphies of continuous characters (characters 0, 1, 2, 4, 9), and other features represent ambiguous synapomorphies. The ambiguous reconstruction is explained by both homoplasy and the absence of lateral extensions in *Araucaria araucana* and *Araucaria angustifolia*, which result in inapplicable scorings for these taxa (e.g., presence of thin bract/scale lateral extensions and epigeal germination and absence of fleshy seedlings). Within this clade, *A. araucana* and *A. angustifolia* (of the South American section *Araucaria*) are sister to a clade including *Araucaria bidwillii* and *Araucaria hunsteinii* (sections *Bunya* and *Intermedia*), in agreement with previous phylogenetic analyses (Setoguchi et al. 1998). Section *Araucaria* is supported by two unambiguous morphological synapomorphies common to all the MPT: a high degree of ovuliferous scale and bract fusion, which results in a relictual ovuliferous scale, or “ligule” (character 19), and the absence of lateral extensions on the bract/scale complexes (character 21). On the other hand, pres-

ence of basally reduced leaves (character 50) is the only unambiguous morphological synapomorphy supporting the monophyly of the *Bunya* + *Intermedia* clade. Also, the morphology of the bract/scale lateral extensions (character 22), which is thin in *A. hunsteinii* and woody in *A. bidwillii* (Stockey 1982), and the germination type (character 42), which is cryptogean in *A. bidwillii* and epigeal in *A. hunsteinii* (Wilde and Eames 1952; Burrows et al. 1992; Burrows and Stockey 1994), represent additional ambiguous morphological synapomorphies of this clade. In particular, the presence of hypogeal germination has been considered the plesiomorphic condition for Araucariaceae (Haines 1983). Nonetheless, the sister group relationship of *A. hunsteinii* and *A. bidwillii*, exclusively supported by the molecular data (fig. 3), rejects the proposed validity of this character as an unambiguous synapomorphy of sections *Araucaria* and *Bunya*. It is interesting to note that by analyzing the morphological data set alone, we recover the monophyly of the clade formed by sections *Araucaria* and *Bunya*, with *A. hunsteinii* as the sister species of this clade, which explains the previous morphologically based theories about the relationships of those species.

Agathis. The monophyly of *Agathis* is strongly supported by molecular, morphological, and combined analyses (fig. 3). The genus is defined by five unambiguous morphological synapomorphies (characters 3, 9, 31, 54, 55), most of which have previously been included in the diagnosis of the genus (Whitmore 1980; Stockey and Taylor 1981; de Laubenfels 1988; Stockey and Atkinson 1993; Stockey 1994). The internal relationships of *Agathis* obtained here are consistent with previous molecular phylogenetic analyses (Setoguchi et al. 1998; Stockler et al. 2002). The basal position of *Agathis australis* and the presence of a clade formed by the species endemics to New Caledonia (i.e., *Agathis montana*, *Agathis ovata*, *Agathis moorei*, *Agathis lanceolata*) are strongly supported by our analyses (fig. 3) and represent the major points of agreement. All the remaining species of the genus are part of a monophyletic group, sister to the New Caledonian clade, which has a broad geographic distribution including Australia, Borneo, Malay Peninsula, Sumatra, Malaysia, and Fiji (Farjon 2010). De Laubenfels (1988) divided *Agathis* in three sections (i.e., *Agathis*, *Rostrata*, and *Prismatobracteata*), basically distinguished by the angle present in the dorsal part of the microsporophyll and the presence or absence of a beak on the bract/scale complex (de Laubenfels 1988). Subsequently, Stockey and Atkinson (1993) demonstrated that the sections are not consistent with morphological and cuticular leaf characters. The results of our analysis, which are defined mostly by the molecular evidence, strongly contradict the monophyly of these sections (fig. 3).

Phylogenetic Position of Fossil Araucariaceae

All of the fossil species included in our analyses formed a clade with extant species of Araucariaceae on both the combined and morphological analyses (fig. 4). These results support that idea that permineralized conifer seed cones preserve enough morphological and anatomical information to support the assignment to the crown group Araucariaceae. A similar hypothesis was tested for other conifer families using a mor-

phological data matrix based on an ovulate cone characters from extant and extinct taxa (Rothwell et al. 2009).

Considering the relationships proposed in this article (figs. 3, 4), Araucariaceae is basally split in two morphologically distinctive clades, *Araucaria* and the agathoid clade. The first accepted record of the genus *Araucaria* dates from the Early Jurassic (Rothwell et al. 2012 and citations therein), and therefore, the first diversification of the family must have occurred at least during this time. The *Araucaria* lineage has a diverse and continuous record across the Mesozoic and Cenozoic, including species with preserved anatomy (some of which were included in this article) and numerous other taxa known from compressions and impressions that have a cosmopolitan distribution (Kendall 1949; Stockey 1975, 1978, 1980a, 1980b; Harris 1979; Hill and Brodribb 1999; Dettmann and Clifford 2005; Kunzmann 2007; Axsmith et al. 2008; Panti et al. 2011). Within Araucariaceae, *Araucaria* is the genus best represented in the fossil record. In particular, its Mesozoic record is notoriously diverse and distributed on both hemispheres. Five of the fossils species included in our analyses, previously assigned to the genus *Araucaria* (table 1), are recovered, forming a monophyletic group with the extant species of *Araucaria* (fig. 4). In addition, *Araucarites bindrabunensis*, suggested to be part of the genus *Araucaria* by Stockey (1982), appears in the same clade. A single unambiguous morphological synapomorphy supports this clade in all the MPT: the absence of seed abscission (character 28). Several ambiguous synapomorphies also support this clade, as noted above for the extant *Araucaria* species. The strict consensus of the MPT shows five of the fossil *Araucaria* species forming a basal polytomy (fig. 4) and *Araucaria sphaerocarpa* as the sister group of the clade formed by all extant species of the genus.

The basal position of all the fossil species of *Araucaria* can be considered preliminary, given that these taxa are almost exclusively represented in our data matrix by information from the ovulate cones. Morphological characters supporting the internal relationships of extant *Araucaria* in our data set are related to all the analyzed structures (e.g., leaves, pollen cones), so that information from different organs in these extinct taxa (i.e., reconstructing “whole plants”) may alter their phylogenetic position. So far, the analyzed information does not support the placement of any of the fossil taxa in the crown group of the genus *Araucaria* or in one of its four sections (table 1). For instance, *Araucaria mirabilis* from the Middle Jurassic of Patagonia (Argentina) and *Araucaria sphaerocarpa* from the Middle Jurassic of England have been repeatedly related to section *Bunya*, given the anatomical and morphological similarities of their ovulate cones (Stockey 1982).

It is interesting to note that recent molecular clock estimates (Crisp and Cook 2011; Leslie et al. 2012) have inferred the divergence of the *Araucaria* crown group to be as old as the Paleogene (Crisp and Cook 2011) or the Paleogene/Late Cretaceous (Leslie et al. 2012). Our results are consistent with these estimates given that all the analyzed fossils are older than the Late Cretaceous but are placed as part of the stem group of *Araucaria*.

In contrast, the fossil record of the agathoid clade is much more scarce and limited to Cretaceous and Cenozoic leaf remains, pollen cones, and pollen (Chambers et al. 1998; Kunzmann 2007). Our analyses support the placement of the extinct

Wairarapaia mildenballii and *Emwadea microcarpa* (table 1) as the stem of the agathoid clade. The close relationship of these species with *Agathis* and *Wollemia* was previously suggested (Cantrill and Rain 2006; Dettmann et al. 2012) based on the numerous shared features in the ovulate cones (e.g., seed winged, free from the bract/scale complex). As we explained before, several of these features represent ambiguous synapomorphies of the agathoid clade. However, the complete fusion of bract and ovuliferous scale (character 19) and the presence of integumentary wings (character 29) on the single seed are unambiguous morphological synapomorphies common to all the MPT. Among the extant species, all the species of *Agathis* are characterized by the presence of two thin membranous integumentary wings. One of them is obliquely placed with respect to the major axis of the seed, whereas the other is rudimentary. On the other hand, the seeds of *Wollemia* are circumferentially winged, and only in some cases (e.g., non-viable seeds) is a slight asymmetry observed (Chambers et al. 1998). The symmetric wings of the seeds of the basal *Emwadea* and *Wairarapaia* indicate that this is the plesiomorphic condition of the agathoid clade, and the asymmetry is interpreted as a synapomorphy of *Agathis*. Future phylogenetic studies may benefit from further studies on the anatomy and morphology of several characters that present variability within this clade (e.g., seed vasculature and insertion) and are often better studied in fossils than in extant taxa (e.g., *Agathis* spp.). Chambers et al. (1998) pointed out that without a detailed knowledge of the morphology of this lineage, several compressions of leaves and cone scales that would normally be assigned to *Araucaria* may be better understood as members of its sister group, the agathoid clade.

Conclusions

Using a combined phylogenetic analysis of molecular and morphological data scored for 39 species of Araucariaceae (31 extant, 8 fossils) and more than 300 outgroups, we have been able to reconstruct a well-supported phylogeny of the conifer family Araucariaceae. The simultaneous analyses support the monophyly of the three extant genera and depict *Araucaria* as the sister group of the agathoid clade formed by *Wollemia* and *Agathis*.

Exploratory analyses conducted on the molecular data set suggest that poor ingroup sampling likely was the main cause of the disagreements on the interrelationships of the three extant genera of Araucariaceae among previous phylogenetic studies.

All main clades within Araucariaceae are supported by at least one morphological synapomorphy, including both discrete and continuous characters. Relationships among extant species of *Araucaria* support the monophyly of the four previously proposed sections of this genus: *Araucaria*, *Bunya*, and *Intermedia* forming a clade that is the sister group of section *Eutacta* (the most speciose section). In contrast, previously suggested sections of the genus *Agathis* were rejected by our results. The monophyly of two New Caledonian clades was obtained, one within *Agathis* and the other within section *Eutacta*. Two groups morphologically diagnosed by leaf size are supported within the New Caledonian clade of *Eutacta*. Six out of eight fossil species included in this study were placed

within the genus *Araucaria* basal to all extant species of the genus. This result, although preliminary, is consistent with recently published molecular node age estimations that inferred the diversification of the crown group of *Araucaria* at the Late Cretaceous–Paleocene. The two remaining fossil species, *Emwadea microcarpa* and *Wairarapaia*, were recovered as the stem group of the agathoid clade.

The results of this first combined analysis of Araucariaceae suggest that the evolutionary histories of *Araucaria* and *Agathis* were markedly different in terms of the timing of the morphological differentiation; whereas the *Araucaria* clade achieved its modern morphology at least by the Middle Jurassic, the evidence presented here suggests that the acquisition of derived traits present in extant species of the agathian clade occurred much later, during the Cretaceous or Paleogene. This difference in the timing of the morphological modernization of the two major lineages of araucariaceous genera also explain the lack of a clear Mesozoic record of *Agathis*, contrasting

with the abundant and well-diagnosable species of *Araucaria* that already had a cosmopolitan distribution during the Jurassic and Cretaceous.

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Appendix A

List of Extant Genera Included in the Phylogenetic Analyses and Number of Species Included for Each Genera

Genera follow an alphabetic order; Araucariaceae genera are indicated in bold.

Abies (21), *Acmopyle* (1), *Actinostrobus* (1), *Afrocarpus* (2), ***Agathis*** (15), *Amentotaxus* (3), ***Araucaria*** (19), *Athrotaxis* (3), *Austrocedrus* (1), *Austrotaxus* (1), *Callitris* (1), *Callitropsis* (1), *Calocedrus* (4), *Cathaya* (1), *Cedrus* (3), *Cephalotaxus* (12), *Chamaecyparis* (5), *Cryptomeria* (2), *Cunninghamia* (2), *Cupressus* (6), *Dacrycarpus* (2), *Dacrydium* (2), *Diselma* (1), *Falcatifolium* (1), *Fitzroya* (1), *Fokienia* (1), *Glyptostrobus* (2), *Halocarpus* (3), *Hesperocyparis* (6), *Juniperus* (12), *Keteleeria* (2), *Lagarostrobos* (1), *Larix* (9), *Lepidothamnus* (2), *Libocedrus* (3), *Manoao* (1), *Metasequoia* (1), *Microbiota* (1), *Microcachrys* (1), *Microstrobos* (2), *Nageia* (1), *Neocallitropsis* (1), *Nothotsuga* (1), *Papuacedrus* (1), *Parasitaxus* (1), *Phyllocladus* (4), *Picea* (33), *Pilgerodendron* (1), *Pinus* (112), *Platyclusus* (1), *Podocarpus* (15), *Prumnopitys* (4), *Pseudolarix* (3), *Pseudotaxus* (1), *Pseudotsuga* (7), *Saxegothaea* (1), *Sciadopitys* (1), *Sequoia* (1), *Sequoiadendron* (1), *Sundacarpus* (1), *Taiwania* (2), *Taxodium* (2), *Taxus* (9), *Tetraclinis* (1), *Thuja* (3), *Thujopsis* (1), *Torreya* (6), *Tsuga* (9), *Widdringtonia* (2), ***Wollemia*** (1), *Xanthocyparis* (1).

List of Extant Ingroup Species and Corresponding GenBank Accession Numbers

Agathis atropurpurea matK: EU025977, rbcL: AF502087, trnD-trnY: EU025984. *Agathis australis* 18s: GU476383, atpB: AY664829, coxI: AF020557, matK: EU025980, nadhB: AY164586, nadhF: AY902169, psbB: AF528892, psbD: AF528919, psbE-psbJ: AF528865, rbcL: AF362993, rpl2: AY664864, rps4: AY188261, trnD-trnY: EU025986. *Agathis borneensis* 18s: D85302, matK: AB023975, rbcL: U96476. *Agathis dammara*, 16s: EU164987, 26s: EU165001, atp1: EU165016, coxI: EU165024, rbcL: U96477, rps4: EU165031. *Agathis lanceolata* atpF et al: FJ173458, matK: AM920134, rbcL: U96481, rpbB: AM920059, rpoc1: AM919788. *Agathis macrophylla* matK: EU025979, rbcL: U87756, trnD-trnY: EU025985. *Agathis microstachya* matK: EU025978. *Agathis montana* matK: AM920135, rbcL: U96478, rpbB: AM920060, rpoc1: AM919790. *Agathis moorei* rbcL: U87755, rpoc1: AM919791. *Agathis ovata* rbcL: U87754, rpoc1: AM919792. *Agathis robusta*, 16s: EU164988, 18s: AF051795, 26s: EU165002, atp1: EU165018, atpB: EF490502, coxI: EU165025, matK: AF456371, nadhB: EF490518, nadhF: EF494250, psbB: EF490512, psbD: EF490506, psbE-psbJ: EF490515, rbcL: U96484, rpl2: EF490521, rps12: EF490518, rps4: EU165032, trnD-trnY: EU025983. *Araucaria angustifolia*, 16s: EU164994, 18s: EU164980, 26s: EU165004, accD: AM919504, atp1: EU165021, coxI: EU165027, matK: EF451975, nadhJ: AM919742, rbcL: U87750, rpoc1: AM919875, rps4: EU165034, trnD-trnY: EU025988, trnH-psbC: AM921999. *Araucaria araucana* 18s: FJ179543, 26s: FJ179544, accD: AM919506, atp1: FJ179547, atpB: DQ646109, atpF et al: FJ173459, coxI: FJ179546, matK: AF543723, nadhJ: AM919743, psbB: AF222701, rbcL: U96467, rpbB: AM920063, rpoc1: AM919872, rps4: FJ179545, trnH-psbC: AM922000. *Araucaria bernieri* accD: AM919511, atpF et al: FJ173461, matK: AM920139, nadhJ: AM919744, rbcL: U96460, rpbB: AM920064, rpoc1: AM919797, trnH-psbC: FJ173519. *Araucaria bidwillii*, 16s: EU164993, 18s: EF673748, 26s: EU165003, accD: AM919512, atp1: EU165022, atpB: AY664830, coxI: EU165026, matK: EU025974, nadhB: AY664816, nadhF: AY902170, psbB: AY664852, psbD: AY664840, psbE-psbJ: AY664846, rbcL: U87751, rpl2: AY664865, rpoc1: AM919877, rps12: AY664816, rps4: EU165033, trnD-trnY: EU025990, trnH-psbC: AM922003. *Araucaria biramulata* accD: AM919516, atpF et al: FJ173464, matK: AM920142, nadhJ: AM919745, rbcL: U96475, rpbB: FJ173763, rpoc1: AM919800, trnH-psbC: FJ173521. *Araucaria columnaris* 18s: AF051794, accD: AM919524, atpF et al: FJ173467, matK: AM920145, nadhJ: AM889583, rbcL:

AM920230, *rpbB*: AM920068, *rpoc1*: AM889861, *trnH-psbC*: FJ173523. *Araucaria cunninghamii*, 16s: EU164990, 18s: AF051792, 26s: EU165005, *accD*: AM919526, *atp1*: EU165020, *atpb*: EF490503, *atpF* et al: FJ173469, *coxI*: EU165028, *matK*: EU025975, *nadhB*: EF490519, *nadhF*: EF494251, *psbB*: EF490513, *psbD*: EF490507, *psbE-psbJ*: EF490516, *rbcl*: U96469, *rpbB*: AM920070, *rpl2*: EF490522, *rpoc1*: GQ436087, *rps12*: EF490519, *rps4*: EU165035, *trnD-trnY*: EU025989, *trnH-psbC*: AM922006. *Araucaria heterophylla*, 16s: EU164991, 18s: AF051793, 26s: EU165006, *accD*: AM919528, *atpF* et al: FJ173470, *coxI*: AF020558, *matK*: AF456374, *rbcl*: U96462, *rpbB*: AM920072, *rpoc1*: AM919873, *rps4*: AY188260, *trnH-psbC*: FJ173525. *Araucaria humboldtensis accD*: AM919532, *atpF* et al: FJ173472, *matK*: AM920150, *rbcl*: U96471, *rpbB*: FJ173765, *rpoc1*: AM919811, *trnH-psbC*: FJ173526. *Araucaria hunsteinii* 18s: GU476386, *accD*: AM919535, *atpF* et al: FJ173473, *matK*: AF456375, *nadhJ*: AM919749, *rbcl*: U87749, *rpbB*: AM920074, *rpoc1*: AM919874, *trnH-psbC*: AM922007. *Araucaria laubenfelsii accD*: AM919539, *atpF* et al: FJ173475, *matK*: AM920153, *rbcl*: U96463, *rpbB*: FJ173766, *rpoc1*: AM919817, *trnH-psbC*: FJ173529. *Araucaria luxurians* 18s: AF051800, *accD*: AM919546, *atpF* et al: FJ173477, *matK*: AM920157, *rbcl*: U96464, *rpbB*: FJ173768, *rpoc1*: AM919823, *trnH-psbC*: FJ173531. *Araucaria montana accD*: AM919548, *atpF* et al: FJ173482, *matK*: AM920159, *rbcl*: U96457, *rpbB*: FJ173771, *rpoc1*: AM919833, *trnH-psbC*: FJ173537. *Araucaria muelleri accD*: AM919557, *atpF* et al: FJ173485, *matK*: AM920162, *nadhJ*: AM919750, *rbcl*: AM920242, *rpbB*: AM920080, *rpoc1*: AM919840, *trnH-psbC*: AM922010. *Araucaria nemorosa accD*: AM919562, *atpF* et al: FJ173487, *matK*: AM920166, *nadhJ*: AM889584, *rbcl*: U96458, *rpbB*: AM920083, *rpoc1*: AM919841, *trnH-psbC*: AM922011. *Araucaria rulei atpF* et al: FJ173488, *matK*: AM920169, *nadhJ*: AM919753, *rbcl*: U96466, *rpbB*: AM920086, *rpoc1*: AM919848, *trnH-psbC*: AM922012. *Araucaria schmidii atpF* et al: FJ173493, *matK*: AM920171, *rbcl*: U96473, *rpbB*: FJ173774, *rpoc1*: AM919853, *trnH-psbC*: FJ173544. *Araucaria scopulorum accD*: AM919587, *atpF* et al: FJ173495, *matK*: AM920175, *rbcl*: U96459, *rpbB*: FJ173776, *rpoc1*: AM919863, *trnH-psbC*: FJ173546. *Araucaria subulata accD*: AM919593, *atpF* et al: FJ173497, *matK*: AM920178, *rbcl*: U96474, *rpbB*: AM920090, *rpoc1*: AM919868, *trnH-psbC*: FJ173549. *Wollemia nobilis*, 16s: EU164992, 18s: GU476384, 26s: EU165007, *atp1*: EU165019, *atpb*: EF490504, *coxI*: EU165029, *matK*: AF456377, *nadhB*: EF490517, *nadhF*: EF494249, *psbB*: EF490511, *psbD*: EF490505, *psbE-psbJ*: EF490514, *rbcl*: AF030419, *rpl2*: EF490520, *rps12*: EF490517, *rps4*: EU165036, *trnD-trnY*: EU025987.

List of Outgroup Species with Family Assignment and Corresponding GenBank Accession Numbers

Cephalotaxaceae: *Cephalotaxus fortunei* 16s: DQ478783, 26s: EU161354, *matK*: FJ600911, *rpoc1*: GQ463570. *Cephalotaxus hainanensis rpoc1*: GQ436160. *Cephalotaxus harringtonii atp1*: DQ646222, *atpb*: DQ646112, *matK*: EF660666, *nadhB*: AY664817, *nadhF*: AY902171, *psbB*: AF528896, *psbD*: AF528923, *psbE-psbJ*: AF528869, *rpl2*: AY664866, *rpoc1*: GQ463577, *rps12*: AY664817. *Cephalotaxus lanceolata matK*: EF660649. *Cephalotaxus latifolia matK*: EF660665. *Cephalotaxus mannii matK*: AB023986, *rpoc1*: GQ463575. *Cephalotaxus oliveri matK*: AF457108. *Cephalotaxus sinensis matK*: AB023988, *rpoc1*: GQ436158.

Cupressaceae: *Actinostrobus acuminatus matK*: AF152175. *Athrotaxis cupressoides atp1*: EU182917, *matK*: AB030131. *Athrotaxis laxifolia matK*: AF152176, *rbcl*: L25754. *Athrotaxis selaginoides atp1*: EU182916, *matK*: AB030130, *rps4*: AY188273. *Austrocedrus chilensis matK*: AF152177. *Callitris rhomboidea matK*: AF152180, *rbcl*: L12537. *Calocedrus decurrens* 18s: D85293, *matK*: AB023982, *rbcl*: L12569, *rps4*: AY188281. *Calocedrus formosana* 18s: D85298, *matK*: FJ475237. *Calocedrus macrolepis* 18s: EF053170, *matK*: AF152179, *rps4*: EF053192. *Calocedrus rupestris* 18s: EU273294. *Chamaecyparis formosensis* 18s: EF673740, *matK*: FJ475234. *Chamaecyparis lawsoniana matK*: FJ475233. *Chamaecyparis obtusa* 18s: EF673741, *matK*: AB030133, *rbcl*: L12570, *rps4*: AY188283. *Chamaecyparis pisifera* 18s: EF053165, 26s: EU161307, *matK*: AB030132. *Chamaecyparis thuyoides matK*: FJ475236. *Cryptomeria japonica* 16s: NC 010548, 18s: D85304, *atp1*: EU182907, *atpb*: NC 010548, *matK*: AF152184, *nadhF*: AP010967, *nadhJ*: AP009377, *psbB*: NC 010548, *psbD*: NC 010548, *rbcl*: AP010967, *rpbB*: AP010967, *rpoc1*: NC 010548, *rps12*: AP010967, *rps4*: AP010967. *Cunninghamia lanceolata* 18s: EU273292, *atp1*: EU182915, *atpb*: AY664833, *matK*: AF152185, *nadhB*: AY664820, *nadhF*: AY902174, *psbB*: AF528898, *psbD*: AF528925, *psbE-psbJ*: AF528871, *rbcl*: AY140260, *rpl2*: AY664869, *rps12*: AY664820, *rps4*: EF053202. *Cupressus cashmeriana matK*: FJ475240. *Cupressus duclouxiana matK*: AF152186. *Cupressus sargentii matK*: AY497215. *Cupressus sempervirens matK*: AF152187, *rbcl*: L12571, *rpoc1*: FN689660. *Diselma archeri matK*: AF152193, *rbcl*: L12572. *Fitzroya cupressoides matK*: AF152194, *rps4*: AY188275. *Fokienia hodginsii* 18s: EU273295, *matK*: AF152195, *rps4*: EF053193. *Glyptostrobus pensilis* 18s: EF053177, *atp1*: EU182909, *matK*: AB030118, *rpoc1*: GQ463580, *rps4*: EF053204. *Juniperus chinensis* 18s: D38243, *atp1*: EU182918, *atpb*: AJ621926, *psbB*: AJ347876, *rpoc1*: GQ463560. *Juniperus communis atpb*: AY664834, *matK*: EU749466, *nadhB*: AY664821, *nadhF*: AY902175, *psbB*: AY664854, *psbD*: AY664842, *psbE-psbJ*: AY664848, *rbcl*: AY664859, *rpbB*: EU749237, *rpl2*: AY664870, *rpoc1*: EU750378, *rps12*: AY664821, *rps4*: AY188279. *Juniperus drupacea matK*: AF152198. *Juniperus formosana* 18s: EF673743, *atp1*: EU182921. *Juniperus phoenicea rpoc1*: FN689655. *Juniperus procera matK*: AF152199. *Juniperus przewalskii* 26s: EU161311. *Juniperus rigida matK*: AB030136, *rbcl*: L12573, *rpoc1*: GQ436200. *Juniperus sabina rps4*: AY188280. *Juniperus virginiana* 16s: U24586, *matK*: EU749468, *rpbB*: EU749241, *rpoc1*: EU750382. *Libocedrus bidwillii matK*: AF152202. *Libocedrus plumosa matK*: AF152200, *rbcl*: L12574. *Libocedrus yateensis matK*: AF152201. *Metasequoia glyptostroboides* 18s: L00970, 26s: EU161306, *atp1*: AF197619, *atpb*: AF469660, *matK*: AF152203, *nadhF*: AF469698, *psbB*: AF469710, *psbD*: AF462406, *psbE-psbJ*: AF469719, *rbcl*: AJ235805, *rpl2*: AF469728, *rpoc1*: GQ463579, *rps12*: AF469736, *rps4*: EF053201. *Microbiota decussata matK*: AF152204, *rbcl*: L12575. *Papuacedrus papuana matK*: AF152206. *Pilgerodendron wiferum matK*: AF152207. *Platycladus orientalis* 18s: EF053168, *atp1*: EU182920, *matK*: AF152208, *rbcl*: L13172, *rpoc1*:

GQ435914, *rps4*: AY188278. *Sequoia sempervirens* 18s: EF053171, *atp1*: EU182913, *atpb*: AJ621927, *matK*: AF152209, *psbB*: AJ347882, *rbcL*: L25755, *rps4*: EF053194. *Sequoiadendron giganteum* *atp1*: EU182919, *matK*: AF152210, *rbcL*: AY056580, *rps4*: AY188267. *Taiwania cryptomerioides* 18s: FJ009673, *atp1*: EU182914, *matK*: AF152211, *rbcL*: L25756, *rps4*: AY188274. *Taxodium distichum* *atp1*: EU182911, *atpb*: AY664835, *matK*: AF152212, *nadhB*: AY664822, *nadhF*: AY902176, *psbB*: AF528915, *psbD*: AF525949, *psbE-psbJ*: AF528888, *rpl2*: AY664871, *rpoc1*: GQ436183, *rps12*: AY664822. *Taxodium mucronatum* 18s: EF053176, *atp1*: EU182908, *matK*: AB030119, *rps4*: EF053203. *Tetraclinis articulata* *matK*: AF152213, *rbcL*: L12576. *Thuja occidentalis* 18s: EF053167, *matK*: AF152214, *rbcL*: L12578. *Thuja plicata* *atpb*: AY664836, *matK*: AF152216, *nadhB*: AY664823, *nadhF*: AY902177, *psbB*: AF528917, *psbD*: AF528942, *psbE-psbJ*: AF528890, *rbcL*: AY237154, *rps4*: AY188276. *Thuja standishii* *matK*: AB030135. *Thujopsis dolabrata* 18s: EF053172, *matK*: AF152217, *rbcL*: L12577, *rps4*: EF053195. *Widdringtonia cedarbergensis* *nadhB*: AY664824, *nadhF*: AY902178, *psbB*: AF528918, *psbD*: AF528943, *psbE-psbJ*: AF528891, *rbcL*: L12538, *rpl2*: AY664872, *rps12*: AY664824. *Widdringtonia schwarzii* *matK*: AF152218. *Xanthocyparis vietnamensis* 18s: EU273293, *matK*: AY380850.

Pinaceae: *Abies alba* 18s: DQ371809, *atpb*: AJ621928, *psbB*: AJ347872. *Abies balsamea* *coxI*: AY159838. *Abies bracteata* 18s: AB026932, *matK*: AF456365. *Abies fabri* 16s: DQ478789, 26s: EU161347, *matK*: AB029657. *Abies fargesii* *matK*: AB029658. *Abies firma* 16s: FJ899565, 18s: AB026933, *matK*: AF143436, *psbB*: FJ899565, *rbcL*: AB015647, *rpbB*: FJ899565, *rps4*: FJ899565. *Abies fraseri* *matK*: AB029660, *rps4*: AY188221. *Abies grandis* 26s: AY056508. *Abies hidalgensis* *matK*: EU269026. *Abies holophylla* *matK*: AF143441. *Abies homolepis* *atp1*: DQ646224, *atpb*: DQ646115, *matK*: AB029662, *rbcL*: AB015648, *rps4*: AY188224. *Abies kawakamii* 18s: EF673728. *Abies koreana* *matK*: AB029663. *Abies lasiocarpa* 18s: X79407, *atpb*: AY664825, *matK*: AB029664, *psbB*: AY664849, *psbD*: AY664837, *psbE-psbJ*: AY664843, *rbcL*: AY664855, *rpl2*: AY664860, *rps12*: AY664813. *Abies magnifica* *rbcL*: X58391. *Abies mariesii* *matK*: AB029665, *rbcL*: AB015650. *Abies nephrolepis* *matK*: AB029666. *Abies numidica* *matK*: AB019864, *rbcL*: AB019827. *Abies sachalinensis* *matK*: AB029667, *rbcL*: AB015651. *Abies sibirica* *matK*: AB029668. *Abies veitchii* *matK*: AB029669, *rbcL*: AB015649. *Cathaya argyrophylla* 18s: AB026934, *matK*: AF143435, *rbcL*: AB019830, *rps4*: EF053197. *Cedrus atlantica* 18s: DQ987891, *matK*: AF143431, *rbcL*: AF145457, *rps4*: EF053196. *Cedrus deodara* 16s: FJ899573, 18s: AB026935, *atp1*: DQ646223, *atpb*: FJ899573, *matK*: FJ899573, *psbB*: FJ899573, *psbD*: AF462401, *psbE-psbJ*: AF469714, *rbcL*: X63662, *rpbB*: FJ899573, *rpl2*: AF469723, *rpoc1*: GQ436205, *rps4*: FJ899573. *Cedrus libani* 18s: AB026937, 26s: AY056507, *atpb*: AJ621929, *psbB*: AJ347873. *Keteleeria davidiana* 16s: NC 011930, 18s: DQ987895, *atpb*: NC 011930, *matK*: NC 011930, *psbB*: NC 011930, *psbD*: NC 011930, *rbcL*: AP010820, *rpbB*: NC 011930, *rps4*: NC 011930. *Keteleeria evelyniana* *matK*: AF143430. *Larix decidua* 18s: AB026938, *matK*: AB019863, *rbcL*: AB019826, *rpoc1*: FN689662. *Larix gmelinii* 18s: EF053173, *matK*: AF143433, *rpoc1*: GQ463587, *rps4*: EF053200. *Larix griffithiana* *atpb*: GU457447. *Larix kaempferi* 18s: D85294, 26s: AY056502, *matK*: AF295028, *rbcL*: AB045038. *Larix laricina* *atpb*: GU457448, *coxI*: AY159845, *matK*: AF295029. *Larix occidentalis* 16s: FJ899578, *atpb*: FJ899578, *matK*: FJ899578, *psbB*: FJ899578, *psbD*: FJ899578, *rbcL*: X63663, *rpbB*: FJ899578, *rps4*: FJ899578. *Larix potaninii* *matK*: AY391402. *Nothotsuga longibracteata* *matK*: AF295030, *rbcL*: AF145459. *Picea abies* *atpb*: AJ001004, *matK*: EU364787, *rbcL*: X75478. *Picea alcoquiana* *rbcL*: AB045041. *Picea asperata* 26s: AY056509, *matK*: AY729946, *rbcL*: AY056578. *Picea brachytyla* *matK*: AY729949. *Picea breweriana* 26s: AY056510, *matK*: AY035197, *rbcL*: AY056579. *Picea chihuahuana* *matK*: AY035198. *Picea crassifolia* *matK*: AY729951. *Picea engelmannii* *matK*: EU364788. *Picea glauca* *coxI*: EU701142, *matK*: EU364790, *rpbB*: EU749245, *rpoc1*: EU750385. *Picea glehnii* *rbcL*: AB045042. *Picea jezoensis* *matK*: EU364792, *rbcL*: AB045045. *Picea koraiensis* *matK*: AY729942. *Picea koyamae* *rbcL*: AB045046. *Picea likiangensis* *matK*: AY786578. *Picea mariana* 18s: L01782, *coxI*: EU701143, *matK*: EU364794, *rpbB*: EU749247, *rpoc1*: EU750386. *Picea maximowiczii* *rbcL*: AB045049. *Picea meyeri* *matK*: AY729948, *rpoc1*: GQ463582. *Picea morrisonicola* 18s: AB026939. *Picea obovata* *matK*: EU199800. *Picea omorika* *matK*: AY035200. *Picea orientalis* *rps4*: AY188225. *Picea pungens* *matK*: EU364795, *rbcL*: X58136. *Picea purpurea* *matK*: AY729950. *Picea retroflexa* *matK*: AY729945. *Picea rubens* *matK*: AF133918, *rps4*: AY188217. *Picea schrenkiana* *matK*: AY786577. *Picea sitchensis* 16s: NC 011152, *atpb*: NC 011152, *matK*: NC 011152, *psbB*: NC 011152, *rbcL*: X63660, *rpbB*: NC 011152, *rps4*: NC 011152. *Picea smithiana* 18s: DQ987890, 26s: EU161351, *matK*: AY729947, *rbcL*: AF145458, *rps4*: AY188226. *Picea spinulosa* *atpb*: AJ621930, *matK*: EU199801, *psbB*: AJ347878. *Picea torano* *rbcL*: AB045051. *Picea wilsonii* *matK*: AY729952, *rpoc1*: GQ463589. *Pinus albicaulis* 16s: FJ899566, *atpb*: FJ899566, *matK*: EF546699, *rbcL*: AB455589, *rpbB*: FJ899566, *rps4*: FJ899566. *Pinus aristata* 16s: FJ899567, *accD*: AM883274, *atpb*: FJ899567, *matK*: FJ899567, *psbB*: FJ899567, *rbcL*: AY115758, *rpbB*: FJ899567, *rpoc1*: AM883458, *rps4*: FJ899567. *Pinus armandii* 18s: EF536360, *accD*: AM883220, *atpb*: FJ899568, *matK*: AB161002, *psbB*: FJ899568, *rbcL*: AB019804, *rpbB*: FJ899568, *rpoc1*: AM883427, *rps4*: FJ899568. *Pinus attenuata* *accD*: AM883206, *atpb*: FJ899569, *matK*: FJ899569, *psbB*: FJ899569, *rbcL*: AB063365, *rpbB*: FJ899569, *rpoc1*: AM883409, *rps4*: FJ899569. *Pinus ayacahuite* *accD*: AM883254, *atpb*: FJ899570, *matK*: AY497257, *psbB*: FJ899570, *rpbB*: FJ899570, *rpoc1*: AM883444, *rps4*: FJ899570. *Pinus balfouriana* *accD*: AM883223, *matK*: AY115799, *rbcL*: X63661, *rpbB*: AM883750, *rpoc1*: AM883430. *Pinus banksiana* *accD*: AM883204, *atpb*: FJ899571, *coxI*: AY159844, *matK*: EU749476, *psbB*: FJ899571, *rbcL*: AB063367, *rpbB*: FJ899571, *rpoc1*: AM883407, *rps4*: FJ899571. *Pinus bhutanica* *matK*: DQ353704. I *accD*: AM883235, *matK*: AB161018, *rbcL*: AB019820, *rpbB*: AM883763, *rpoc1*: AM883437. *Pinus bungeana* *accD*: AM883231, *matK*: AY729953, *rbcL*: AY115761, *rpbB*: AM883759, *rpoc1*: AM883435. *Pinus canariensis* *accD*: AM883262, *atpb*: FJ899572, *matK*: AB084494, *psbB*: FJ899572, *rbcL*: AB019823, *rpbB*: FJ899572, *rpoc1*: AM883449, *rps4*: FJ899572. *Pinus caribaea* *accD*: AM883238, *matK*: AB080942, *rbcL*: AB063385, *rpbB*: AM883766, *rpoc1*: AM883426. *Pinus cembra* *accD*: AM883270, *atpb*: FJ899574, *matK*: DQ353705, *psbB*: FJ899574, *rbcL*: AB019795, *rpbB*: FJ899574, *rpoc1*: AM883717, *rps4*: FJ899574. *Pinus cembroides* *accD*: AM883257, *matK*: AY115785, *rbcL*: AY115753, *rpbB*: AM883785, *rpoc1*:

AM883399. *Pinus clausa* accD: AM883203, matK: AB161003, rbcL: AB161023, rpbB: AM883728, rpoc1: AM883405. *Pinus contorta* 16s: NC 011153, accD: AM883209, atpb: NC 011153, matK: AB080921, psbB: NC 011153, rbcL: AB063369, rpbB: NC 011153, rpoc1: AM889926, rps4: NC 011153. *Pinus coulteri* matK: AY724751, rbcL: AB097777. *Pinus cubensis* matK: AB080938, rbcL: AB063370. *Pinus culminicola* accD: AM883215, matK: AY115776, rbcL: AY115748, rpbB: AM883740, rpoc1: AM883421. *Pinus dalatensis* matK: EF546708. *Pinus densata* accD: AM883224, matK: AB097779, rbcL: AB097770, rpbB: AM883751, rpoc1: AM883431. *Pinus densiflora* matK: AB084497, rbcL: AB019814. *Pinus devoniana* accD: AM883256, matK: AY497277, rpbB: AM883784, rpoc1: AM883446. *Pinus discolor* matK: AY115780, rbcL: AY115745. *Pinus douglasiana* accD: AM883239, matK: AB080925, rbcL: AB063388, rpbB: AM883767, rpoc1: AM883702. *Pinus durangensis* matK: AY497276. *Pinus echinata* accD: AM883266, matK: AB080936, rbcL: AB081077, rpbB: AM883794, rpoc1: AM883715. *Pinus edulis* accD: AM883218, matK: AY115766, rbcL: X58137, rpbB: AM883743, rpoc1: AM883425. *Pinus elliottii* 18s: AF051798, accD: AM883213, matK: AB080931, rbcL: AB081075, rpbB: AM883738, rpoc1: AM883417. *Pinus engelmannii* accD: AM883214, matK: AB080927, rbcL: AB080915, rpbB: AM883739, rpoc1: AM883419. *Pinus fenzeliana* matK: AB161005, rbcL: AB161025. *Pinus flexilis* 16s: FJ899576, accD: AM883207, atpb: FJ899576, matK: EF546711, psbB: FJ899576, rbcL: AB455587, rpbB: FJ899576, rpoc1: AM883690, rps4: FJ899576. *Pinus gerardiana* 16s: NC 011154, accD: AM883530, atpb: NC 011154, matK: NC 011154, psbB: NC 011154, rbcL: AY115762, rpbB: NC 011154, rpoc1: AM883695, rps4: NC 011154. *Pinus glabra* accD: AM883260, matK: DQ353712, rpbB: AM883788, rpoc1: AM883448. *Pinus greggii* accD: AM883253, matK: AY497282, rpbB: AM883781, rpoc1: AM883711. *Pinus halepensis* accD: AM883261, matK: AB081089, rbcL: AB019819, rpbB: AM883789, rpoc1: AM883714. *Pinus hartwegii* accD: AM883252, matK: AB161019, rbcL: AB161043, rpbB: AM883780, rpoc1: AM883428. *Pinus heldreichii* accD: AM883269, matK: AB161006, rbcL: AB019821, rpbB: AM883797, rpoc1: AM883716. *Pinus herrerae* accD: AM883240, matK: AB080943, rbcL: AB063386, rpbB: AM883768, rpoc1: AM883703. *Pinus hwangshanensis* matK: AB161007, rbcL: AB019812. *Pinus jaliscana* accD: AM883241, rpbB: AM883769, rpoc1: AM883704. *Pinus jeffreyi* accD: AM883268, matK: AB080926, rbcL: AB080914, rpbB: AM883796. *Pinus kesiya* matK: AB161008, rbcL: AB019813. *Pinus koraiensis* 16s: NC 004677, accD: AM883197, atpb: NC 004677, matK: NC 004677, psbB: NC 004677, rbcL: AB019797, rpoc1: AM883686, rps4: AY228468. *Pinus krempfii* 16s: NC 011155, atpb: NC 011155, matK: NC 011155, psbB: NC 011155, rbcL: X63665, rpbB: NC 011155, rps4: NC 011155. *Pinus lambertiana* accD: AM883225, atpb: FJ899577, matK: AY497260, psbB: FJ899577, rpbB: FJ899577, rpoc1: AM883694, rps4: FJ899577. *Pinus lawsonii* matK: AB097784, rbcL: AB097771. *Pinus leiophylla* accD: AM883242, atpb: FJ899575, matK: FJ899575, psbB: FJ899575, rbcL: AB063380, rpbB: FJ899575, rpoc1: AM883439, rps4: FJ899575. *Pinus longaeva* accD: AM883528, matK: AY115797, rbcL: X58132, rpbB: AM883747, rpoc1: AM883692. *Pinus luchuensis* 18s: D38246, matK: AB097780, rbcL: AB097772. *Pinus lumholtzii* matK: AY497278. *Pinus massoniana* 16s: DQ478790, accD: AM883205, matK: AB081088, rbcL: AB019815, rpbB: AM883730, rpoc1: AM883689. *Pinus maximartinezii* accD: AM883243, matK: AY115790, rbcL: AY115755, rpbB: AM883771, rpoc1: AM883705. *Pinus maximinoi* accD: AM883258, matK: AB161010, rbcL: AB161040, rpbB: AM883786, rpoc1: AM883447. *Pinus merkusii* 16s: FJ899579, atpb: FJ899579, matK: AY497287, psbB: FJ899579, rbcL: AB019811, rpbB: FJ899579, rps4: FJ899579. *Pinus monophylla* matK: AY115768, rbcL: AY115741. *Pinus montezumae* accD: AM883244, matK: AY497269, rbcL: AB161041, rpbB: AM883772, rpoc1: AM883440. *Pinus monticola* 18s: AY527222, accD: AM883216, atpb: FJ899580, matK: AY497259, psbB: FJ899580, rbcL: AB019799, rpbB: FJ899580, rpoc1: AM883423, rps4: FJ899580. *Pinus morrisonicola* 18s: EF673732, accD: AM883228, matK: AY497263, rpbB: AM883756, rpoc1: AM883433. *Pinus mugo* 26s: AY056500, accD: AM883271, matK: AB081087, rbcL: AB063372, rpbB: AM883799, rpoc1: AM883454. *Pinus muricata* accD: AM883211, matK: AB080935, rbcL: AB063387, rpbB: AM883736, rpoc1: AM883414. *Pinus nelsonii* accD: AM883250, matK: AY115793, rbcL: AY115757, rpbB: AM883778, rpoc1: AM883709. *Pinus nigra* matK: AB084498, rbcL: AB019817, rpoc1: FN689663. *Pinus occidentalis* matK: AY497281. *Pinus oocarpa* accD: AM883246, matK: AB081084, rbcL: AB063382, rpbB: AM883773, rpoc1: AM883707. *Pinus palustris* accD: AM883265, matK: AB080937, rbcL: AB063373, rpbB: AM883793, rpoc1: AM883452. *Pinus parviflora* 16s: FJ899581, accD: AM883272, atpb: FJ899581, matK: FJ899581, psbB: FJ899581, rbcL: AB019800, rpbB: FJ899581, rpoc1: GQ249002, rps4: FJ899581.

Pinus patula accD: AM883248, matK: AB080944, rbcL: AB063381, rpbB: AM883776, rpoc1: AM883441. *Pinus peuce* 16s: FJ899582, 26s: AY056499, atpb: FJ899582, matK: AY497254, psbB: FJ899582, rbcL: AB019803, rpbB: FJ899582, rps4: FJ899582. *Pinus pinaster* 16s: FJ899583, accD: AM883264, atpb: FJ899583, matK: FJ899583, psbB: FJ899583, rbcL: AB019818, rpbB: FJ899583, rpoc1: AM883451, rps4: FJ899583. *Pinus pinceana* accD: AM883251, matK: AY115788, rbcL: AY115754, rpbB: AM883779, rpoc1: AM883443. *Pinus pinea* accD: AM883263, matK: AB084496, rbcL: X58133, rpbB: AM883791, rpoc1: AM883700. *Pinus ponderosa* 16s: FJ899555, accD: AM883227, atpb: FJ899555, matK: FJ899555, psbB: FJ899555, rbcL: AB063374, rpbB: FJ899555, rpoc1: AM883696, rps4: FJ899555. *Pinus praetermissa* matK: DQ353711. *Pinus pringlei* matK: AY497283. *Pinus pseudostrobus* accD: AM883249, matK: AY497268, rpbB: AM883777, rpoc1: AM883442. *Pinus pumila* accD: AM883267, matK: AB161013, rbcL: AB019796, rpbB: AM883795, rpoc1: AM883453. *Pinus pungens* matK: AB080932, rbcL: AB063375. *Pinus quadrifolia* matK: AY115771, rbcL: AY115744. *Pinus radiata* accD: AM883232, matK: AB080934, rbcL: X58134, rpbB: AM883760, rpoc1: AM883698. *Pinus remota* matK: AY115775, rbcL: AY115750. *Pinus resinosa* accD: AM883276, atpb: FJ899556, matK: FJ899556, psbB: FJ899556, rbcL: AB063384, rpbB: FJ899556, rpoc1: AM883460, rps4: FJ899556. *Pinus rigida* accD: AM883277, matK: AB080929, rbcL: AB063376, rpbB: AM883805, rpoc1: AM883720. *Pinus roxburghii* accD: AM883222, matK: AB084495, rbcL: AB019824, rpbB: AM883749, rpoc1: AM883429. *Pinus rzedowskii* accD: AM883259, atpb: FJ899557, matK: FJ899557, psbB: FJ899557, rbcL: AY115756, rpbB: FJ899557, rpoc1: AM883713, rps4: FJ899557. *Pinus sabiniana* accD: AM883275, matK: AY497272, rpbB: AM883803, rpoc1: AM883719.

Pinus serotina matK: AY724753, rbcL: AB081076. *Pinus sibirica* atpb: FJ899558, matK: FJ899558, psbB: FJ899558, rbcL: AB455590, rpbB: FJ899558, rps4: FJ899558. *Pinus squamata* 16s: FJ899559, atpb: FJ899559, matK: FJ899559, psbB: FJ899559, rbcL: AY115763, rpbB: FJ899559, rps4: FJ899559. *Pinus strobiformis* matK: EF546726, rbcL: AB455588. *Pinus strobus* 26s: AY056501, accD: AM883210, atpb: FJ899560, coxI: AY159843, matK: FJ899560, psbB: FJ899560, rbcL: AB019798, rpbB: FJ899560, rpoC1: EF590648, rps4: FJ899560. *Pinus sylvestris* accD: AM883233, coxI: EU701151, matK: AB097781, rbcL: AB019809, rpbB: EU749255, rpoC1: AM883699. *Pinus tabuliformis* accD: AM883202, matK: AB161015, rbcL: AB019810, rpbB: AM883727, rpoC1: AM883688. *Pinus taeda* 16s: FJ899561, accD: AM883200, atpb: FJ899561, matK: AB080928, psbB: FJ899561, rbcL: AB063377, rpbB: FJ899561, rpoC1: AM883687, rps4: FJ899561. *Pinus taiwanensis* 18s: EF673731, accD: AM883208, matK: AB161016, rbcL: AB161045, rpbB: AM883733, rpoC1: AM883410. *Pinus teocote* matK: AB097783, rbcL: AB097773. *Pinus thunbergii* 16s: FJ899562, accD: AM883273, atpb: FJ899562, matK: FJ899562, psbB: FJ899562, psbD: NC 001631, rpbB: FJ899562, rpoC1: AM883456, rps4: FJ899562. *Pinus torreyana* accD: AM883229, atpb: FJ899563, matK: AY497273, psbB: FJ899564, psbD: FJ899564, rpbB: FJ899564, rpoC1: AM883697, rps4: FJ899564. *Pinus tropicalis* matK: AB080920, rbcL: AB063378. *Pinus uncinata* matK: AB097778, rbcL: AB097774. *Pinus virginiana* accD: AM883212, matK: AB080923, rbcL: AB063379, rpbB: AM883737, rpoC1: AM883415. *Pinus wallichiana* 18s: X75080, matK: AY734482, rbcL: X58131, rpoC1: GQ436203, rps4: AY188212. *Pinus yunnanensis* accD: AM883199, matK: AB161017, rbcL: AB019816, rpbB: AM883724, rpoC1: AM883401. *Pseudolarix amabilis* 18s: DQ987896, matK: AB019866, rbcL: AB019829, rps4: EF053198. *Pseudotsuga japonica* atpb: GU457444. *Pseudotsuga macrocarpa* atpb: GU457445. *Pseudotsuga menziesii* 18s: AB026941, 26s: AY056498, atpb: AY664826, coxI: AY159841, matK: AF143439, psbB: AY664850, psbD: AY664838, psbE-psbJ: AY664844, rbcL: AY664856, rpl2: AY664861, rps12: AY664814, rps4: AY188223. *Pseudotsuga sinensis* 18s: EF673733, atpb: GU457443. *Tsuga canadensis* 18s: AB026942, 26s: AY056511, atpb: AJ235632, coxI: AY159839, matK: AF143438, rbcL: AY056581, rps4: AY188220. *Tsuga caroliniana* matK: EF395576, rps4: AY188219. *Tsuga chinensis* 18s: AB026943, matK: EF395586, rbcL: AF145462. *Tsuga diversifolia* matK: EF395589. *Tsuga dumosa* 18s: DQ987893, matK: EF395593, rbcL: AF145460. *Tsuga forrestii* matK: EF395596, rbcL: AF145461. *Tsuga heterophylla* matK: EF395598, rbcL: X63659. *Tsuga mertensiana* 18s: AB026945, matK: DQ166027, rbcL: AF145463, rps4: AY188215. *Tsuga sieboldii* matK: EF395605.

Podocarpaceae: *Acmopyle pancheri* 18s: AF342758. *Afrocarpus falcatus* 18s: AF342759, matK: AF457111, rbcL: X58135, rps4: AY188254. *Afrocarpus gracilior* 18s: AF342757, atpb: AJ621932, psbB: AJ347881. *Dacrycarpus dacrydioides* 18s: U87303. *Dacrycarpus imbricatus* 16s: DQ478784, 18s: D38247, rps4: DQ478805. *Dacrydium cupressinum* 18s: U87304, matK: AF457112, rps4: AY188255, trnD-trnY: EU025992. *Falcatifolium papuanum* 18s: AF342756. *Halocarpus bidwillii* 18s: AF342754. *Halocarpus biformis* 18s: AF342762. *Halocarpus kirkii* matK: AF457117. *Lagarostrobos franklinii* 18s: U87298, rps4: AY188253. *Lepidothamnus intermedius* rps4: AY188256. *Lepidothamnus laxifolius* 18s: AF342755, matK: AF457114. *Manoao colensoi* 18s: AF342753. *Microcachrys tetragona* 18s: U87299. *Nageia nagi* 16s: DQ478786, 18s: D16447, 26s: EU161315, matK: AB023990, rpoC1: GQ463565, rps4: AY188248. *Parasitaxus usta* 18s: AF342765. *Phyllocladus aspleniifolius* 18s: DQ629434, atp1: DQ646219, atpb: DQ646110, rps4: AY188258. *Phyllocladus hypophyllus* 18s: U87300. *Phyllocladus trichomanoides* 18s: D38244, 26s: EU161339, atpb: AJ621931, matK: AF456376, psbB: AJ347877. *Podocarpus archboldii* 18s: GU476464. *Podocarpus costalis* 18s: D38473. *Podocarpus cunninghamii* 18s: GU476465. *Podocarpus elatus* 18s: AF051796, matK: AF457113. *Podocarpus henkelii* rps4: AY188249. *Podocarpus latifolius* rps4: AY188250. *Podocarpus macrophyllus* 26s: DQ008664, atp1: AF197620, matK: AF228111, rpoC1: GQ436050. *Podocarpus matudae* rps4: AY188251. *Podocarpus milanjianus* atpb: AJ235567. *Podocarpus nakaii* 18s: EF673746. *Podocarpus neriifolius* 16s: DQ478787. *Podocarpus novae-caledoniae* 18s: AF342766. *Podocarpus salignus* rps4: AY188252. *Podocarpus totara* 18s: U87301. *Prumnopitys ferruginea* 18s: AF342761, matK: AF457115, trnD-trnY: EU025991. *Prumnopitys harmsiana* 18s: AF342763. *Prumnopitys laevis* 18s: AF342764. *Prumnopitys taxifolia* 18s: U87295, rps4: AY188259. *Saxegothaea conspicua* 18s: U87294, atpb: AY664828, matK: AF457116, nadhB: AY664815, nadhF: AY902168, psbB: AY664851, psbD: AY664839, psbE-psbJ: AY664845, rbcL: AY664857, rpl2: AY664863, rps12: AY664815. *Sundacarpus amarus* 18s: AF342752.

Sciadopityaceae: *Sciadopitys verticillata* 18s: D85292, 26s: EU161318, atp1: DQ646220, atpb: AF239792, matK: AB023994, nadhB: AF238076, nadhF: AF469700, psbB: AY116650, psbD: AF239793, psbE-psbJ: AY007486, rbcL: L25753, rpl2: AY007499, rps12: AF238076, rps4: AY188262.

Taxaceae: *Amentotaxus argotaenia* 16s: DQ478774, 18s: DQ478809, atp1: EU161459, matK: AF152219, rbcL: L12580, rps4: DQ478797. *Amentotaxus formosana* matK: AB023977, rpoC1: GQ463562, rps4: AY188265. *Amentotaxus yunnanensis* 16s: DQ478775, atp1: EU161461, matK: AB023981, rpoC1: GQ435989, rps4: DQ478798. *Austrotaxus spicata* matK: AF456378. *Pseudotaxus chienii* 16s: DQ478776, 18s: DQ478807, atp1: EU161457, matK: AF456379. *Taxus baccata* 16s: DQ478777, 26s: EU161462, atp1: EU161456, matK: DQ478791, rpoC1: FJ395859, rps4: X84145. *Taxus brevifolia* atpb: AF528864, matK: EU078561, nadhB: AY664818, nadhF: AY902172, psbB: AF528916, psbD: AF525948, psbE-psbJ: AF528889, rpl2: AY664867. *Taxus canadensis* coxI: AY159840, matK: EF660661, rpoC1: GQ435986. *Taxus cuspidata* 16s: DQ478779, atp1: EU161455, matK: AF228104, rpoC1: GQ435985, rps4: DQ478801. *Taxus floridana* matK: EF660652. *Taxus globosa* matK: EF660647. *Taxus wallichiana* 16s: DQ478778, atp1: EU161453, matK: DQ478792, rpoC1: GQ435988, rps4: DQ478802. *Torreya californica* atpb: AJ621934, matK: AB023998, nadhB: AY664819, nadhF: AY902173, psbB: AY664853, psbD: AY664841, psbE-psbJ: AY664847, rbcL: AY664858, rpl2: AY664868, rpoC1: GQ436161, rps12: AY664819. *Torreya fargesii* matK: AF228107, rpoC1: GQ436162. *Torreya grandis* 16s: DQ478781, atp1: EU161460, matK: AF228108, rpoC1: GQ463592, rps4: DQ478803. *Torreya jackii* matK: EF660667. *Torreya nucifera* 16s: DQ478782, atp1: EU161458, matK: AB024003, rpoC1: GQ463573, rps4: DQ478804. *Torreya taxifolia* matK: AF457110, rps4: AY188263.

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